

## TOWARD COMPREHENSIVENESS: INCREASED MOLECULAR SAMPLING WITHIN CYPRAEIDAE AND ITS PHYLOGENETIC IMPLICATIONS

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### ABSTRACT

This paper introduces 73 additional taxa to the existing mitochondrial molecular database of 202 taxa for the Cypraeidae and addresses the systematic implications of their inclusion. Five outgroup members from the Ovulidae are also added. Sequence data are included from all previously missing extant named genera (*Propustularia*, *Barycypraea* and *Schilderia*), completing the overall “generic-level” framework for living cowries. Newly added taxa include 47 recognized species, 25 subspecies, and six undescribed taxa. Phylogenetic results generally are consistent with previous arrangements, with few minor adjustments. The most significant findings are that: (1) currently recognized *Nesiocypraea* is broken into two disparate clades, a deeply rooting *Nesiocypraea sensu stricto* group and the more derived *Austrasiatica* (Lorenz, 1989). (2) Two newly included *Barycypraea* taxa are sister to *Zoila*, reaffirming the validity of the subfamilial clade Bernayinae. (3) The inclusion of a significant number of added *Erroneini* taxa (N = 24) creates a phylogenetic challenge because of poor support and recovered relationships inconsistent at first glance with traditionally recognized affinities. In order to maintain nomenclatural consistency, *Erronea* is maintained at a generic level, whereas *Adusta* is dropped to subgeneric status within *Erronea*. Greater than 90% of currently recognized species are included, and 93% of these are supported by molecular criteria. Moreover, more than 70% of the tested, recognized subspecies are distinct. The phylogeny provides one of the most comprehensive, species-level frameworks to date for testing diversification theories in the marine tropics.

Key words: Cypraeidae, molecular systematics, taxon sampling, *Cypraea*.

### INTRODUCTION

Cowries (Gastropoda: Cypraeidae) are taxonomically one of the best known of all molluscan groups, and have been used frequently to examine speciation and biogeographic patterns in the marine tropics (Schilder, 1965, 1969; Foin, 1976; Kay, 1984, 1990; Meyer, 2003). A wealth of taxonomic (Schilder & Schilder, 1938, 1971; Schilder, 1939; Lorenz & Hubert, 1993; Groves, 1994; Lorenz, 2002), anatomical (Troschel, 1863; Vayssi re, 1923, 1927; Riese, 1931; Risbec, 1937; Schilder, 1936; Kay, 1957, 1960, 1963, 1985, 1996; Bradner & Kay, 1996; Lorenz, 2000), biogeographic (Schilder, 1965, 1969; Foin, 1976; Burgess, 1985; Liltved, 1989; Lorenz & Hubert, 1993; Lorenz, 2002) and fossil data (Schilder & Schilder, 1971; Kay, 1990, 1996; Groves, 1994) is available for the group; however, what has been lacking is a well-resolved, comprehensive species-level phylogeny.

These phylogenetic hypotheses of relationship establish sister pairs at the appropriate taxonomic level and provide the framework to test diversification theories. Meyer (2003) introduced molecular data for 234 taxa in Cypraeidae and generated phylogenetic hypotheses for most major clades as well as sister-group relationships for most species. Systematics for Cypraeidae were reviewed in light of the results and diversification patterns within the tropics were addressed. The study presented herein significantly increases the comprehensiveness of taxon sampling in the group by introducing 73 Cypraeidae and five Ovulidae taxa to the existing molecular dataset and discusses their systematic implications. In addition to broader taxonomic sampling, this paper presents the results of broader geographic sampling. The appendix lists 147 localities added across the various taxa. Five outgroup taxa from six localities are included, and 67 recognized cypraeid species or subspecies are added from 75 locali-

ties. The remaining 66 localities were added to supposedly known taxa, but revealed six previously unrecognized taxa, some of which may correspond to names currently in synonymy upon review of type localities.

## MATERIALS AND METHODS

### Recognition Criteria: ESU versus OTU

The ultimate goal of this project is to construct a comprehensive phylogeny of cypræid gastropods at the appropriate level for diversification studies. As such, the operational taxonomic unit (OTU) chosen for phylogenetic analyses generally represents an evolutionarily significant unit (ESU) that must fulfill some minimal criteria established through genetic scrutiny. First, mtDNA haplotypes of sampled individuals must represent a monophyletic clade; yet this alone is not sufficient, because any phylogeny has a plethora of monophyletic groups, because a clade requires only two individuals. Thus, auxiliary criteria are required to delineate significant units. Within cowries, these additional criteria are (1) geographic distinction or allopatry, (2) significant genetic distance from the sister group such that pairwise distance comparisons yield a bimodal distribution, and/or (3) taxonomic recognition by previous workers. An OTU is included in analyses only if at least two of these three criteria are met. Most OTUs fulfill all three criteria and are considered evolutionarily significant units (ESUs) (*sensu* Moritz, 1994). These criteria are erected in order to delineate independent evolutionary trajectories, but do not guarantee that the units are reproductively isolated. In a few instances, two of the three criteria (genetic separation and taxonomic recognition) are not supported by the third (exclusive geographic signatures). While the genetic differences (monophyly) between populations indicate some independent period of evolutionary history between geographic regions, it appears that, on occasion, haplotypes from outlying regions can mix back into the sister gene pool. The few cases where all three criteria are not fulfilled always occur on the periphery of regions (e.g., Marquesas, Hawaii) and show asymmetrical, "downstream", dispersal events (Fig. 1). As circumscribed, all ESUs discussed indicate independent evolutionary histories, but alternative criteria, such as either nuclear markers or breeding experiments, are needed to verify reproductive isolation.

### Molecular Methods

Most methods follow protocols detailed in Meyer (2003) for all aspects of preservation, extraction, amplification, and sequencing. Tissue samples were acquired from a variety of

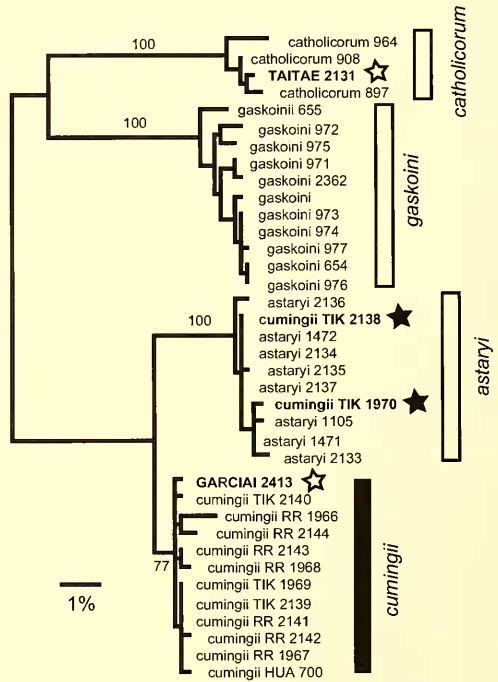


FIG. 1. ESU vs. OTU criteria. Phylogram showing the relationships among members of the Pacific *Cribrarula* subclade, with bootstrap values for major groups. Four distinct clades are evident, and the names presented on the right: *Cribrarula catholicorum*, *C. gaskoini*, *C. astaryi*, and *C. cumingii*. Note that single individuals of two newly included taxa, *C. taitae* and *C. garciai* (white stars), nest within two of the major clades and show little variation (a single mutation). These two new taxa are introduced as OTUs, because of their distinct morphology and geography (American Samoa and Easter Island, respectively), but are currently not considered ESUs by molecular criteria. All individuals from the Marquesas are *C. astaryi*; however, two individuals of *C. cumingii* possess haplotypes belonging to the *C. astaryi* clade as well (dark stars). While the two haplotype clusters are distinct, the pattern indicates uni-directional exchange of larvae downstream from the Marquesas (*C. astaryi*). Molecular criteria recognize these two clades as ESUs with historically limited exchange. (TIK = Tikehau, RR = Rangiroa, HUA = Huahine, all *C. astaryi* from Marquesas, all *C. gaskoini* from Hawaii, and all *C. catholicorum* from Solomon Islands)

sources and locations (listed in the acknowledgements and appendix). Most samples were preserved in 95% ethanol. DNA extraction was performed using DNAzol (Chomczynski et al., 1997) using one-half volumes and following the manufacturer's protocol (Molecular Research Center, Inc.) with the exception that the digestion step was increased by an additional 24 or 48 h. PCR was performed as described in Meyer (2003). COI primers were as follow (from Folmer et al., 1994): LCO-1490 (5'-3') GGT CAA CAA ATC ATA AAG ATA TTG G, and HCO-2198 (5'-3') TAA ACT TCA GGG TGA CCA AAA ATC A. For problematic taxa, these primers were de-generated as follows: dgLCO-1490 (5'-3') GGT CAA CAAATC ATAAAG AYA TYG G, and dgHCO-2198 (5'-3') TAAACT TCA GGG TGA CCA AAR AAY CA. Two internal primers were designed for small amplifications of degraded DNA: InCypLCO (5'-3') CGT YTA AAT AAT ATAAGY TTY TG, and InCypHCO (5'-3') CGT ATA TTA ATA ATT GTT GTA AT. Palumbi's (1996) 16Sar and 16Sbr primers were used for 16S: 16Sar (5'-3') CGC CTG TTT ATC AAA AAC AT, and 16Sbr (5'-3') CCG GTC TGAATC CAG ATC ACG T. Two internal primers were designed for small amplifications of degraded DNA: In16Sar (5'-3') GGG CTA GTA TGAATG GTT TGA, and In16Sbr (5'-3') ATG CTG TTA TCC CTATGG TAA CT. The polymerase chain reaction was carried out in 50  $\mu$ l volumes, using 1  $\mu$ l of template. Each reaction included 5  $\mu$ l 10X PCR buffer, 5  $\mu$ l dNTPs (10mM stock), 2  $\mu$ l of each primer (10 $\mu$ M stock), 3  $\mu$ l MgCl<sub>2</sub> solution (25 mM stock), 0.2  $\mu$ l Taq (5 Units/ $\mu$ l stock) and 31.8  $\mu$ l ddH<sub>2</sub>O. Reactions were run for 35-40 cycles with the following parameters: an initial one min denaturation at 95°C; then cycled at 95°C for 40 sec (denaturation), 40°C to 44°C (COI) or 50°C to 54°C (16S) for 40 sec (annealing), and 72°C for 60 sec (extension). Successfully amplified products were cleaned for cycle sequencing using Wizard<sup>®</sup> PCR Preps (Promega). Sequencing also followed Meyer (2003) with all new sequences generated using ABI chemistry and sequencers. Sequences were generated from the resulting electrophenograms using Sequencher (Gene Codes).

All primer sequences, aligned COI and 16S sequences and Nexus files are available at the archived data web pages of the Florida Museum of Natural History Malacology Department (<http://www.flmnh.ufl.edu/malacology/archdata/Meyer2004>), and new sequences are deposited in Genbank under accession numbers AY534351 through AY534503.

## Phylogenetic Analyses

The 297 operational taxonomic units (OTUs) presented in this paper were selected from an extensive database comprised of over 2,000 sequenced individuals. In general, taxa are included if they exhibit distinctive geographic and/or genetic signatures. In most instances, new OTUs are recognized in the literature as either species (N = 47) or subspecies (N = 25). This paper introduces six previously unrecognized taxa.

The increasing size of this dataset presents computational and heuristic challenges for phylogenetic analyses. Two weighted transversion bias parsimony searches (3:1 and 5:1) were performed on the complete dataset using PAUP\* (Swofford, 1998). At first, 250 random-addition replicate searches were performed, but with a tree limit of ten imposed to minimize search time on suboptimal islands. After 250 replicates, the most parsimonious topologies were used as starting trees for exhaustive searches without tree limits. This strategy was employed for both weighted analyses, and the most parsimonious topologies were pooled and evaluated using likelihood criteria. ModelTest v. 3.06 (Posada & Crandall, 1998) was used to select the most appropriate model for likelihood parameters. The most likely weighted parsimonious trees were then compared using consensus methods.

A two-tiered, compartmentalized strategy was adopted that followed Meyer (2003) for levels of topological support. The strict consensus topology derived from the most likely overall analyses was divided into four subequal components called basal, mid1, mid2, and derived. Because the basal, mid1 and mid2 cohorts are necessarily paraphyletic groups that include the common ancestor and some, but not all, of its descendants, representative derived clades were included in the paraphyletic analyses. In this way multiple derived member clades overlapped between more basal and derived analyses, and the overall topology could be "scaffolded" together by linking clades shared in both basal and derived compartments.

Within each of the four subanalyses, parsimony searches were performed using a 5:1 transversion bias. Both bootstrap (Felsenstein, 1985) analyses (1,000 replicates) and decay (Bremer, 1994) analyses (TreeRot v2; Sorenson, 1999) were performed to establish levels of support. Results from Bayesian meth-

ods (Mr. Bayes v3.04b) are not reported in this paper, but were generated for the four subgroups and compared to the combined parsimony/likelihood methods utilized in PAUP\*. Overwhelmingly, they were consistent with the results presented here, but on few occasions differed in hypotheses of relationship. The scaffolded parsimony global topologies were compared to the scaffolded Bayesian topology using likelihood criteria in PAUP\*. The combined topology derived from the compartmentalized Bayesian subsets was less likely than the overall topologies found using the combined parsimony/likelihood criteria. It appears that Bayesian results depended on taxon sampling and outgroup inclusion. While this finding may be of interest to the general systematic community, it is not a point specifically addressed in this paper.

## RESULTS

The final culled dataset contained 297 OTUs and 1,107 characters, 493 base pairs from 16S and 614 bases from COI. For 16S, alignment followed those presented in Meyer (2003) based on secondary structure. Weighted parsimony searches resulted in 512 equally most parsimonious trees (MPTs) for 3:1 Ti:Tv and 480 trees for 5:1 searches. Derived portions of the comprehensive topology were consistent. Thus, all named clades (subfamilies, tribes and genera) presented in Figure 2 are found in all topologies, except one mentioned below. However, the topologies recovered from alternate weightings differed in five deeper regions, all of which are poorly supported regardless of methodology. First, 5:1 topologies placed the clade consisting of *Propustularia/Nesiocypraea/Ipsa* basal as sister to all other cowries. In 3:1 topologies this clade moves up one node and is sister to Erosariinae. Second, the pustulose clade consisting of *Nucleolaria/Cryptocypraea/Staphylaea* is monophyletic in 5:1 trees, while in 3:1 topologies these genera are a basal paraphyletic grade leading to the clade including *Monetaria/Perisserosa/Erosaria*. Third, in 5:1 topologies *Perisserosa* is sister to *Erosaria*, whereas in 3:1 trees, *Perisserosa* is sister to *Monetaria*. Fourth, the arrangement of major groups along the backbone from Umbilliini to Cypraeovulinae conflicts. Results from 5:1 searches are shown in Figure 2, whereas in 3:1 topologies, *Notocypraea* and *Cypraeovula* (Cypraeovulinae) are a basal sister grade leading to more derived member groups. Finally, the basal arrangement within Erroneini is dif-

ferent. In 3:1 topologies *Purpuradusta* is more basal, while in 5:1 trees, *Erronea* is more basal.

When alternative topologies were evaluated using ModelTest, the GTR+I+G model was selected as the best-fit model. When both the 3:1 MPTs and 5:1 MPTs were evaluated using the selected likelihood criteria [Iset base = (0.315128 0.136452 0.111915), Nst = 6, Rmat = (0.99559 41.36057 1.0461 1.68935 22.78834), rates = gamma, shape = 0.562423, Pinvar = 0.48426], the 5:1 subset was significantly more likely (ANOVA:  $p < 0.001$ , average  $-\ln$  likelihood = 49513.8). Therefore, results from the 5:1 searches are presented herein.

The overall relationships among major subgroups recovered in the 5:1 MPTs are more consistent with both morphological and fossil evidence in addition to being more likely based on molecular data. In particular, a monophyletic pustulose clade is more parsimonious for conchological and anatomical features, because it is more likely that a bumpy shell was derived a single time, rather than being derived either twice independently, or derived once then lost. Also, the basal, paraphyletic status of *Notocypraea* and *Cypraeovula* within the 3:1 topologies is inconsistent with the fossil record for both groups relative to more derived members of the 3:1 MPTs (i.e., *Umbilia*, *Baryocypraea*, and *Zoila*), which appear earlier in the record and root more deeply in the 5:1 topologies. Also, the sister-group relationship of the two genera is more consistent with paleobiogeography (the breakup of Gondwanaland) and recognized affinities based on both conchological and developmental criteria. The other major discrepancies between the 3:1 and 5:1 MPTs (most basal cowries, *Perisserosa* affinities, and position of *Purpuradusta*) are more ambiguous based on alternate criteria (morphological or paleontological).

### Suprageneric Relationships (Fig. 2)

Overall, suprageneric results were consistent with previous systematic findings (Meyer, 2003), with two exceptions. First, *Ipsa* falls outside Erosariinae and is no longer sister to Erosariini, but instead is allied with newly included *Propustularia* and *Nesiocypraea sensu stricto*. New sequence data from *Nesiocypraea teramachii neocaledonica* did not result in an affinity with other recognized "*Nesiocypraea*" species (*N. hirasei*, *N. sakurai* and *N. langfordi*). Instead, *Nesiocypraea teramachii* roots more deeply in the phylogeny as a distant sister to *Ipsa childreni*, within a clade that includes both *Ipsa* and *Propustularia*. Thus, the inclusion of

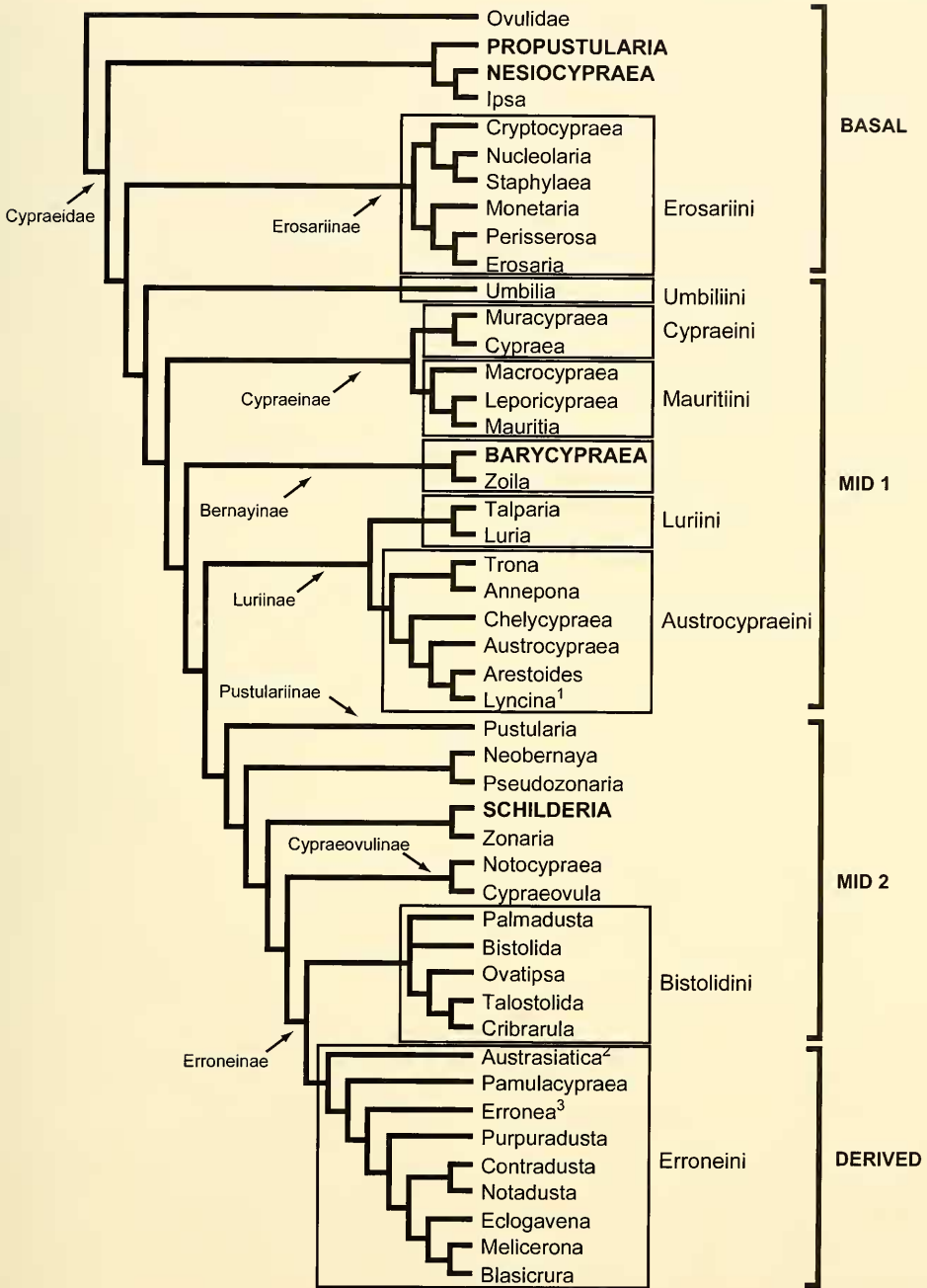


FIG. 2. Strict suprageneric consensus topology of 480 most parsimonious trees derived from a 5:1 Ti:Tv weighted search strategy of all 297 OTUs. Subfamilies are indicated with arrows and tribes are listed to the right. The four compartments for further subanalyses are bracketed to the right. The four newly added genera are capitalized and bolded. <sup>1</sup>*Lyncina* includes the subclades *Callistocypraea*, *Miolyncina* and *Lyncina* as reported in Meyer (2003). <sup>2</sup>*Austrasiatica* replaces the prior use of *Nesiocypraea* for the same clade. <sup>3</sup>*Erronea* now includes *Adusta*, formerly recognized as the sister taxon.

two new ancient lineages (*Propustularia* and *Nesiocypraea*) affects the relative position of *Ipsa*. Moreover, the finding that *Nesiocypraea teramachii* is not related to other previously recognized *Nesiocypraea*, compels me to recognize the clade *Austrasiatica* proposed by Lorenz (1989) at the generic level for the group including *Austrasiatica hirasei*, *A. sakurai*, and *A. langfordi*. There are some conchological and anatomical features that support this separation. The left posterior terminal ridge in *Nesiocypraea* is more produced and separate from the body of the shell, whereas in *Austrasiatica*, the ridge is continuous with the body. Lorenz (pers. comm.) also states that (1) *Nesiocypraea* lacks a distinct embryonic banding, having instead only a darker middorsal zone, (2) *Nesiocypraea* have a proportionally larger spire, and (3) the darker pattern of the shell is absent in juvenile *Austrasiatica*, only gained after the deflection of the labral margin; whereas, the darker pattern can be part of juvenile *Nesiocypraea* shells. Additionally, the rachidian tooth of *Nesiocypraea* lacks the prominent paired basal denticles present in the three *Austrasiatica* taxa, and the tooth shape is less elongated and squared, whereas the rachidian in *Austrasiatica* narrows toward the cusps (Bradner & Kay, 1996). The fact that *Austrasiatica* was erected to differentiate the three species (albeit incorrectly aligned with *Schilderia*) is also an indication that the two lineages possess independent histories. The deep position of *Propustularia* within the cowrie phylogeny is not surprising because it is one of the oldest of extant taxa, extending back to the Lower Eocene (Kay, 1996).

The second suprageneric difference concerns the relative position of *Zoila* in the overall phylogeny and is caused by the inclusion of sequence data for two taxa from the ancient lineage *Barycypraea*. These new data indicate that *Barycypraea teulerei* and *Barycypraea fultoni* are sister taxa, and they are sister to *Zoila*. This *Barycypraea*/*Zoila* clade is recognized as the extant members of the subfamily Bernayinae, a group that includes many extinct fossil members and extends back into the Mesozoic (Kay, 1996). These new data change the relative position of *Zoila* to Cypraeinae (Meyer, 2003); however, the topology in this region of the phylogeny is poorly supported.

The final suprageneric addition to the molecular database is the inclusion of sequence data from *Schilderia achatidea*, the single, living representative from an older, more diverse genus of European affinities. Previously, the paraphyletic arrangement of the genera

*Pseudozonaria* and *Zonaria* was a surprising result (Meyer, 2003). These new data for *Schilderia* place the genus as sister to *Zonaria* to the exclusion of *Pseudozonaria* (and *Neobernaya*), and phylogenetic results maintain their independent, paraphyletic status. These findings are more consistent with geographic affinities than recognized taxonomic affinities (*Pseudozonaria* is often considered a subgenus of *Zonaria*), as both *Neobernaya* and *Pseudozonaria* are currently restricted to the eastern Pacific whereas *Schilderia* and *Zonaria* are restricted to the western Atlantic.

### Basal Compartment (Fig. 3)

Five Ovulidae taxa are added in these analyses: *Pseudocypraea exquisita*, *Volva volva*, *Primovula concinna*, *Dentiovula takeoi*, and *Prosimnia semperi*. Within Ovulidae, only a few major clades are well supported and may be the results of poor taxon sampling. First, the clade Eocypraeinae appears well supported and includes *Pedicularia*, *Jenneria* and *Pseudocypraea*. Eocypraeinae is sister to a strongly supported clade (Ovulinae) that includes the remaining Ovulidae. Within the Ovulinae, two subgroups are well supported and represent the major clades Volvini and Ovulini. Of the added Ovulidae, *Volva* falls into Volvini, but *Prosimnia* unexpectedly falls into Ovulini as do *Primovula* and *Dentiovula*. These results are generally consistent with Cate's (1974) arrangement of higher-level relationships within the Ovulidae. *Cyphoma gibbosum* falls basal to these two sisters in the strict consensus topology; however, its position is poorly supported, and it is expected to move within the Volvini with the inclusion of more taxa. Monophyly of Ovulidae is not addressed herein and would require the inclusion of more distant representatives from Lamellaridae, Triviidae and Eratoidea.

The Cypraeidae basal group includes the genera *Propustularia*, *Nesiocypraea*, *Ipsa*, *Cryptocypraea*, *Nucleolaria*, *Staphylaea*, *Monetaria*, *Perisserosa*, and *Erosaria*. *Propustularia*, *Nesiocypraea*, and *Ipsa* form a clade that roots deeply within the phylogeny and is sister to all other cowries. Each of the three genera is represented by only a single taxon, and only *Nesiocypraea* contains additional recognized species missing from the dataset (*Nesiocypraea midwayensis*, *N. lisetae* and *N. aenigma*). While sharing a most recent common ancestor, the three genera are highly divergent from each other, representing significant periods of independent history. Two

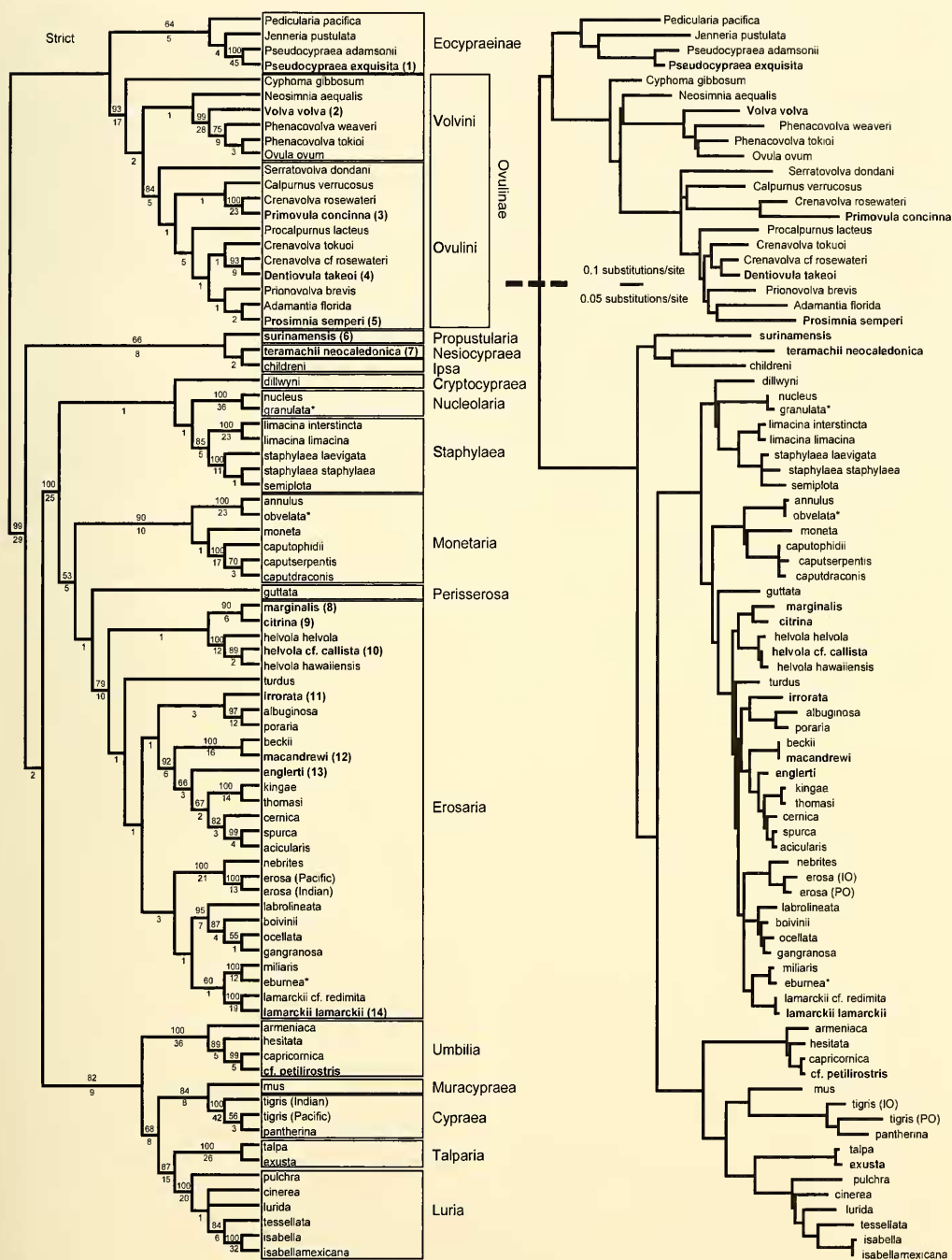


FIG. 3. Basal Compartment cladogram and phylogram. Bootstrap values are presented above branches in the cladogram and rescaled decay values below. Bolded taxa are new additions to the data set. Their identity number shown in parentheses follows the listing in the Appendix. Generic or suprageneric groupings are indicated to the right of the cladogram. OTUs with an asterisk (\*) are not ESUs based on molecular criteria. Phylogram to the right is based on likelihood distances using a GTR+I+G model of sequence evolution. Note that the scaling for branch lengths changes between Ovulidae and Cypraeidae.

are known exclusively from the Indo-Pacific (*Nesiocypraea* and *Ipsa*) and one (*Propustularia*) from the western Atlantic, but has a fossil record from North America, the Caribbean, and Europe (Kay, 1996). The splits among these ancient groups are among the earliest of all extant species and may have occurred in the Mesozoic. While reasonably supported as a clade, this basal group is not strongly supported as the most basal sister, and in other analyses (3:1) moves up to become sister of the remaining basal taxa (Erosariinae).

The final six genera from the basal compartment form the strongly supported clade Erosariinae and is the sister group to all remaining extant species. Membership and relationships within the Erosariinae are consistent with previous findings (Meyer, 2003). Five taxa from *Erosaria* are added: *Erosaria marginalis*, *E. citrina*, *E. helvola* cf. *callista*, *E. macandrewi*, and *E. engleri*. Ten independent lineages are strongly supported (bootstraps > 90/decays > 6) within *Erosaria*, but interrelationships among them are not (< 50/< 4). *Erosaria marginalis* and *E. citrina*, both from the western Indian Ocean, are strongly supported as sister taxa. This clade is poorly supported as sister to the *E. helvola* complex. Within *Erosaria helvola*, three ESUs are identifiable: *E. helvola hawaiiensis* from Hawaii, *E. helvola* cf. *callista* from the Marquesas, and *E. helvola helvola* from the remainder of the IndoPacific. The newly included ESU, *E. helvola* cf. *callista*, may need a new name, because the type locality of *E. helvola callista* is Tahiti (Shaw, 1909), not the Marquesas. These five taxa are sister to the remaining *Erosaria*; however, the basal position is poorly supported. *Erosaria turdus* is a monotypic, deeply divergent lineage. Newly added *Erosaria irrorata*, a species restricted to the oceanic islands of the Pacific, is poorly supported as sister to a strongly supported clade (97/12) including *E. albuginosa* and *E. poraria*. These three taxa are sister to a well-supported lineage (92/6) of eight taxa that I tentatively recognize as *Paulonaria* at the subgeneric level. New sequence data from *Erosaria macandrewi*, a Red Sea taxon, closely ally that species with *E. beckii*. These two species are sister to the remaining *Paulonaria* taxa. The final additional taxon within *Paulonaria* is *Erosaria engleri*, a species endemic to Easter Island and Sala y Gomez. *Erosaria engleri* shares a more recent common ancestor with the remaining five *Paulonaria* taxa. All other relationships within *Erosaria* are the same as those presented in Meyer (2003) and are indicated in Figure 3. Newly added haplotypes from *E. lamarckii*

*lamarckii* populations of the western Indian Ocean exhibit a recent divergence from the previously recorded *E. lamarckii* cf. *redimita* of the Andaman Sea. One final finding from additional *Erosaria* sequence data is that haplotypes from *Erosaria miliaris* and *E. eburnea* individuals interfinger, indicating that either the divergence between these two taxa is very recent and lineage sorting has not occurred, or that these two taxa represent a cline across the western Pacific from a colored dorsum in the west to white shells in the east.

#### Mid1 Compartment (Fig. 4)

The second paraphyletic compartment contains mostly large-shelled taxa from the following tribes: Umbiliini, Cypraeini, Mauritiini, Luriini, Austrocypraeini, and the genus *Pustularia*. All six clades are well supported (> 70/> 5) except for Austrocypraeini. As in Meyer (2003), interrelationships among these major suprageneric clades are resolved in the consensus, but poorly supported. Austrocypraeini and Luriini are sisters and recognized as the subfamily Luriinae. *Barycypraea* and *Zolla* are sisters and recognized as the subfamily Bernayinae. Cypraeini and Mauritiini are sisters and recognized as the subfamily Cypraeinae. In the current topology, *Pustularia* and all remaining cowries share a more recent common ancestor. This large clade is sister to Luriinae, which in turn is sister to Bernayinae, and this inclusive clade is sister to Cypraeinae. As in Meyer (2003), Umbiliini is sister to all remaining mid1, mid2 and derived taxa.

Within the mid1 compartment, 13 taxa are added to the sequence database. The first addition falls within the genus *Umbilia* and is tentatively recognized as *Umbilia* cf. *petilirostris*. A single divergent sequence was generated from tissue samples collected from the deep waters in the Capricorn Channel off Queensland, Australia. Seven sequenced individuals were completely identical, while an eighth sample from a subadult shell was significantly divergent. This single sample may represent the newly described *Umbilia petilirostris* Darragh, 2002; however, authors disagree on its taxonomic status (Wilson & Clarkson, in press). Until more comprehensive sampling is done in the region, I present the divergent sequence as a different ESU, which does not preclude it from being lumped within *U. capricornica* at a later date with more exhaustive sampling. The relationships within *Umbilia* remain as in previous analyses (Meyer, 2003).

The second taxon added to mid1 is *Leporicypraea mappa aliwalensis* from Natal, South



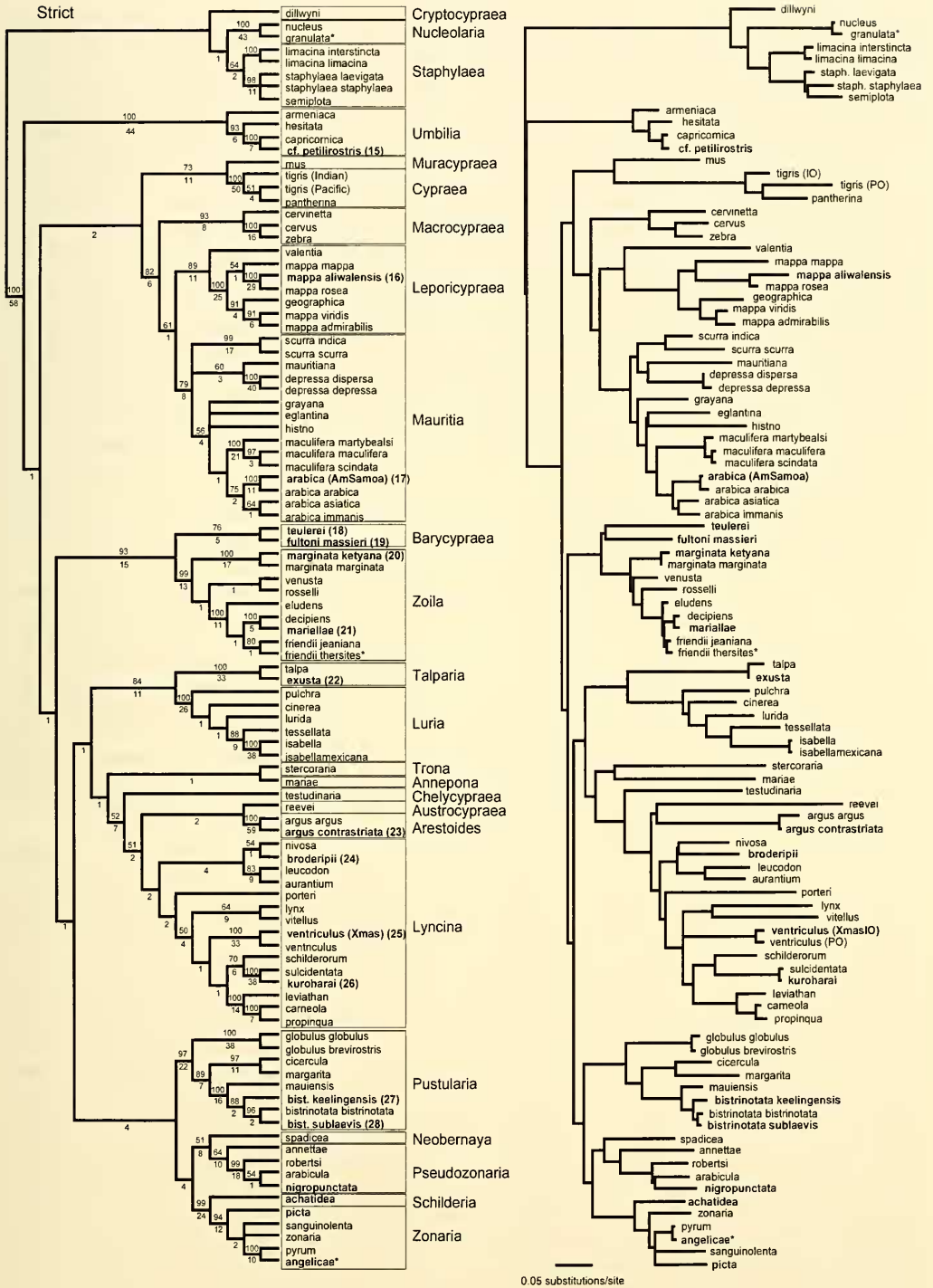


FIG. 4. Mid 1 Compartment cladogram and phylogram. All other information as in Fig. 3.

Africa, and falls as sister to *Leporicypraea mappa rosea*. Lorenz (2002) has recently revised the taxonomy of the *mappa* group in light of molecular findings. Importantly, the names I associated previously with ESUs have changed, and those changes are reflected in the Appendix and also discussed herein. The taxon I previously recognized as *Leporicypraea mappa viridis* from SE Polynesia is now recognized as *Leporicypraea admirabilis*. The taxon I previously recognized as *Leporicypraea mappa panerythra* from the non-continental portions of the western Pacific is now recognized as *Leporicypraea mappa viridis*. The other taxon names remain the same. Sequences of *L. mappa "rewa"* from Pacific localities (Fiji, Vanuatu, Palau, and South China Sea) interfinger with haplotypes of *L. mappa geographica* individuals from Indian Ocean localities (NW Australia, Phuket, Seychelles, and Zanzibar). Therefore, I recognize only a single taxon, *L. mappa geographica*, for this clade. Because of its conchological distinctiveness and sympatry with conspecifics, Lorenz (2002) elevated *L. mappa geographica* to specific status with Indian and Pacific subspecies. Based on the genetic difference between *mappa*-complex conspecifics and geographic overlap, specific status is certainly acceptable. However, the remaining *L. mappa* subspecies are paraphyletic. The phylogeny Lorenz (2002: 27) presents is correct and reflects this arrangement. Certainly, other recognized cowrie species are derived from paraphyletic parent species (e.g., *Eclogavena coxeni* and others; see Meyer, 2003: table 4, and cases herein), and *L. geographica* would have to be added to this list. These results suggest a third species sister to *L. geographica* should be recognized that would include both *L. mappa viridis* and *L. mappa admirabilis*. *L. mappa geographica* individuals have been found sympatrically with both *L. mappa mappa* and *L. mappa viridis* individuals in the Pacific Ocean. However, as yet, *L. mappa mappa* and *L. mappa viridis* haplotypes have not been found together.

One new undescribed taxon is added to *Mauritia*. Haplotypes of *M. arabica* individuals from American Samoa cluster independently from haplotypes of *M. arabica* individuals from other Pacific localities. Shells from Samoan individuals tend to be smaller, more heavily margined and more circular than individuals from other Pacific localities. Results from increased sampling in both *M. depressa depressa* (N = 10) and *M. depressa dispersa* (N = 10) maintain their independent, reciprocally monophyletic status, albeit recently diverged. As in

previous findings, the interrelationships among major lineages in *Mauritia* are poorly supported. Consensus methods and poor support result in two polytomies (Fig. 4). Further genetic data will be needed to address this region of the phylogeny as all extant taxa have been sampled.

New sequence data from *Barycypraea teulerei* and *B. fultoni* place them as sister taxa and align them with the genus *Zoila* to form the group Bernayinae. Sequence data presented for *Barycypraea fultoni* are of *B. fultoni amorimi* from Mozambique. The Australian *Zoila marginata* complex is split into two ESUs as increased sampling indicates fixed molecular differences between populations separated by the Southwest Cape region between capes Naturaliste and Leeuwin. Further sampling directly within this region may uncover intermediate haplotypes that would link the two ESUs and suggest a cline instead of two independent lineages. Such a finding is the case in the *Zoila friendii* complex. However, as none have been discovered yet, I present the data as two tentative ESUs: *Zoila marginata marginata* to the south and *Z. marginata ketyana* to the west. Other described *Z. marginata* taxa (Lorenz, 2001; 2002) within each ESU interfinger, and do not fulfill molecular criteria for recognition. Sequence data from *Zoila mariellae* are the final addition to the Bernayinae clade. While the exact provenance of the animal sequenced is unknown, it is likely from the northwestern shelf of Australia. Molecular results place *Z. mariellae* as a distinct sister to *Z. decipiens*, also from the northwestern shelf, as expected.

Following along the phylogeny, the clade Luriinae comes next. *Talparia* and *Luria* are strongly supported as the clade Luriini. A small fragment from 16S was amplified from a degraded *Talparia exusta* specimen, and as expected, the taxon is sister to the more widespread *Talparia talpa*. Surprisingly, sequence divergence between the two species appears to be relative small, indicating a more recent divergence than expected. Better-preserved material from *T. exusta* is needed before these relative results can be confidently assessed. The inclusion of four new taxa to the Austrocypraeini (*Arestoides argus contrastriata*, *Lyncina broderipii*, *L. ventriculus* from the Indian Ocean, and *L. kuroharai*) does not help in resolving interrelationships among member taxa. *Arestoides argus* is broken into a Pacific clade, *A. argus argus*, and a western Indian Ocean clade, *A. argus contrastriata*, based on additional sequence data from the Indian Ocean. *Lyncina broderipii* appears as sister to *L. nivosa* within the *Callistocypraea* clade, as

predicted in Meyer (2003). A single sampled individual of *L. ventriculus* from Christmas Island in the Indian Ocean falls significantly outside the haplotype cluster of individuals (N = 6) from various regions of the Pacific basin. *Lyncina ventriculus* is an oceanic taxon, and because of the geographic gap between sites across continental Southeast Asia, I choose to present the Christmas Island form as new, undescribed, distinct ESU. Further sampling of individuals from Christmas Island may change this interpretation, but they are currently lacking. A single sample of *Lyncina kuroharai* was sequenced and the results place it closely related to *L. sulcidentata*, an endemic Hawaiian taxon. The shallow split between these two taxa indicates a relatively recent common ancestor. Faunal ties have been documented in other cowrie species between Hawaii and Japan, most notably in *Luria isabella*, and the close affinities between *L. kuroharai* and *L. sulcidentata* represent another example of this biogeographic link.

The final two ESUs added within the mid1 compartment are members of the genus *Pustularia*, and more specifically are recognized subspecies of *Pustularia bistrinotata*. A single *P. bistrinotata keelingensis* individual was sequenced, is distinct, and appears as sister to the remaining *P. bistrinotata* complex. Furthermore, *P. bistrinotata sublaevis* individuals (N = 5) from southeast Polynesia (Tuamotu and Societies) cluster together, forming a third ESU within *P. bistrinotata*.

#### Mid2 Compartment (Fig. 5)

The third phylogenetic compartment, mid2, contains members from the genera *Neobernaya*, *Pseudozonaria*, *Schilderia*, *Zonaria*, the subfamily Cypraeovulinae, and the tribe Bistolidini of the subfamily Erroneinae. Interrelationships among member clades are consistent with previous findings (Meyer, 2003). *Neobernaya* and *Pseudozonaria* are sisters, and that clade is sister to the remaining cowries. The inclusion of sequence data from the genus *Schilderia* (*S. achatidea*), place the group as sister to *Zonaria*, and together this clade shares a more recent ancestor with the remaining taxa. The subfamily Cypraeovulinae includes both the South African *Cypraeovula* and South Australian *Notocypraea* and is sister to the western IndoPacific Erroneinae, which is composed of two tribes: Bistolidini and Erroneini.

Within the mid2 compartment, 25 taxa are added to the existing sequence database; at

least one ESU is added within each genus except the monotypic *Neobernaya*. *Pseudozonaria nigropunctata*, a Galapagos endemic, falls into the eastern Pacific clade as a divergent sister to *P. arabicula*, although not strongly supported. The position of *Schilderia achatidea* has been mentioned previously as sister to *Zonaria*, now found exclusively in the eastern Atlantic. Two taxa are added from *Zonaria*. *Zonaria picta* from the Cape Verde Islands falls near the base of *Zonaria*, and its relationship with other Zonarid taxa is ambiguous, resulting in a polytomy at the base of the group. Alternative phylogenetic reconstructions at the base of the group show small internodes, indicative of a short radiative burst, with little divergence since. New sequence data from *Pseudozonaria angelicae* are extremely similar to haplotypes from *P. pyrum* (both *P. pyrum angolensis* and *P. pyrum senegalensis*). I include *P. angelicae* as a taxon in the phylogeny, but prefer to consider it at most a subspecies until further sequence data are available within the *P. pyrum* complex, as I have reservations concerning divergences along the mostly continuous West African/Mediterranean coastline.

Sequence data from six additional taxa are included within Cypraeovulinae, two from *Notocypraea* and four from *Cypraeovula*. In *Notocypraea*, I tentatively recognize two ESUs within *Notocypraea angustata*, with a phylogenetic break somewhere between Port Lincoln and Port Macdonnell, South Australia. Two divergent haplotype clusters exist without intermediate states. Again, further data may change this interpretation, but at present I chose to represent these as different ESUs indicating distinct evolutionary trajectories. Sequence data from a single specimen of *Notocypraea hartsmithi*, a rare species from southeastern Australia, indicate that the species is sister to all remaining *Notocypraea* taxa. Within *Cypraeovula*, four taxa are added, but their inclusion does not change previous interpretations that the group is composed of predominately four divergent lineages with minor differences within each. New sequence data from both *Cypraeovula fuscobrunnea* and *C. fuscodentata* closely align these taxa with *C. capensis*. New sequence data from *C. mikeharti* and *C. algoensis* closely align those taxa with *C. edentula* and *C. alfredensis*. Noting the shallow divergences among recognized species in Figure 5, I am doubtful that many of the described subspecies within *Cypraeovula* (summarized in Lorenz, 2002) will fulfill my molecular criteria for ESU status. As some species are differentiated currently by only a

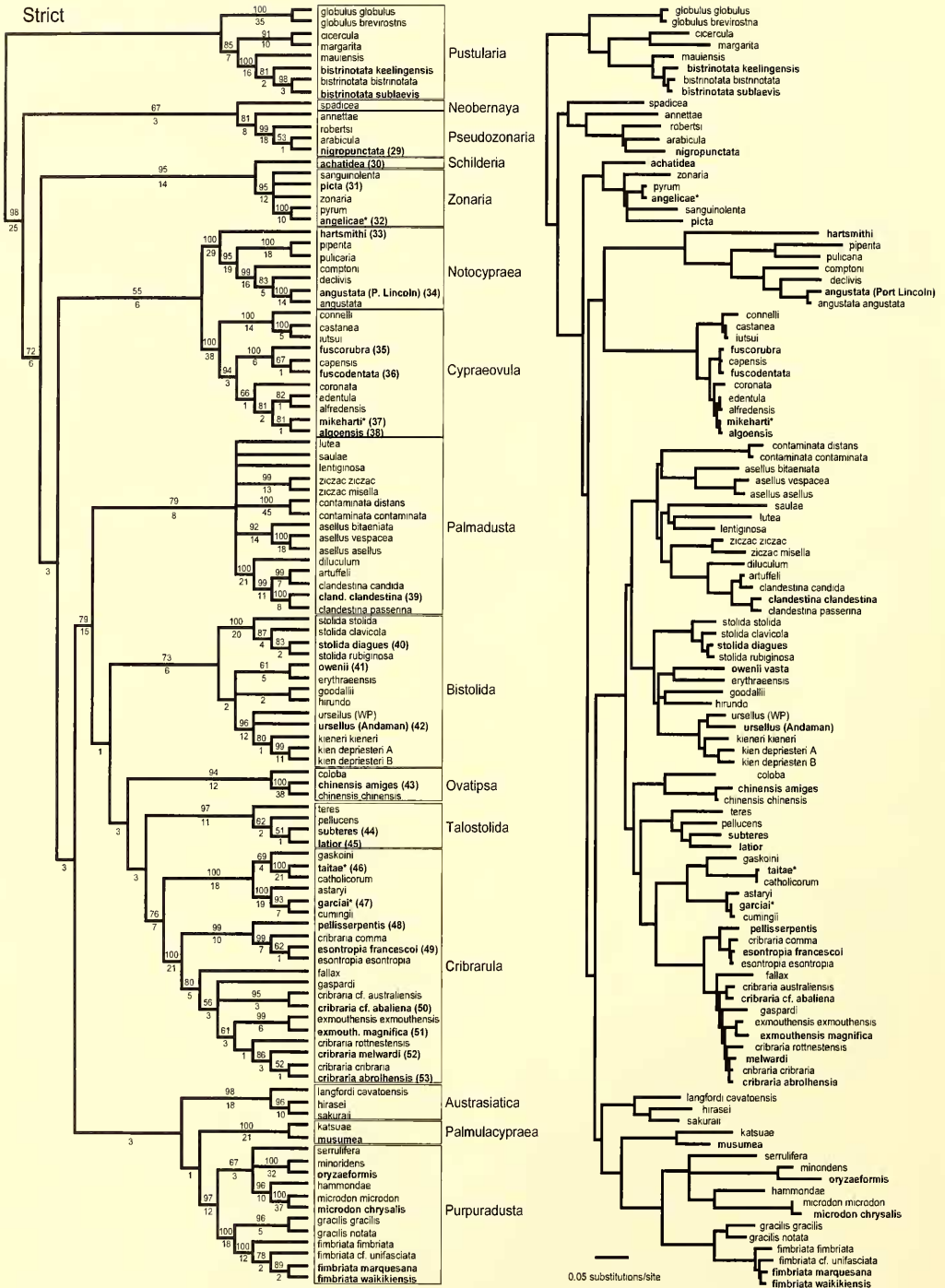


FIG. 5. Mid 2 Compartment cladogram and phylogram. All other information as in Fig. 3.

single mutation (e.g., *Cypraeovula mikeharti*/*C. algoensis* or *C. castanea*/*C. iutsui*), there simply is not enough room for differences to have accumulated between taxa. This is not to say that described entities are not independent. Indeed, because *Cypraeovula* taxa are direct developers with limited dispersal and gene flow, regional differences are expected on small geographic scales, much like the South Australian endemic clades *Umbilia*, *Zoila*, and *Notocypraea*. However, based on the genetic similarity among sampled member *Cypraeovula*, much of this variation has to be very recently derived. This pattern is borne out in the South Australian direct developers that have been more extensively sampled.

The tribe Bistolidini within Erroneinae is composed of members from five genera: *Palmadusta*, *Bistolida*, *Ovatipsa*, *Talostolida* and *Cribrarula*. As in Meyer (2003), the basal root of Bistolidini is poorly resolved. Overall analyses place either *Palmadusta* as sister to the other four genera or *Palmadusta* and *Bistolida* as a clade, sister to the remaining three. Compartmentalized analyses place *Palmadusta* at the base, although poorly supported. The addition of 15 ESUs did not help in resolving this issue. Only one taxon is added to the *Palmadusta* clade, but it alters the subspecific designations previously ascribed (Meyer, 2003). New haplotypes from Andaman Sea *P. clandestina* individuals form a distinct monophyletic clade. This new ESU is sister to the western Indian Ocean *P. clandestina passerina*, and the two of them are sister to the Pacific *P. clandestina* clade and the Japanese endemic *P. artuffeli*. Based on a review of *P. clandestina* subspecies and type localities, the Pacific clade that I had formerly (Meyer, 2003) recognized as *P. clandestina clandestina* should be *P. clandestina candida*, and the new *P. clandestina* clade from the Andaman Sea now bears the name *P. clandestina clandestina*. I also reviewed the subspecies and type localities for the three *P. asellus* ESUs previously unnamed (Meyer, 2003). Based on increased sampling and conchological comparisons, I tentatively ascribe the following subspecific designations for the three clades: *P. asellus asellus* for the western Indian Ocean clade, *P. asellus vespacea* for the Seychelles to western Pacific clade, and *P. asellus bitaeniata* for the Melanesian and Pacific clade (Fig. 5, Appendix). Unfortunately, the addition of *P. clandestina clandestina* does not help in resolving the basal nodes of *Palmadusta*. As shown in Figure 5, the base of *Palmadusta* is poorly resolved and sister group assignments are ambiguous. A few

lineages remain strongly supported (*P. asellus*, *P. clandestina/diluiculum*, *P. ziczac* and *P. contaminata*), but confident hypotheses of other interrelationships require further data.

Three taxa are added to *Bistolida*: *B. stolidia diagues*, *B. owenii* and an undescribed, distinct eastern Indian Ocean clade of *B. ursellus*. Individuals of *B. stolidia diagues* from the Seychelles fall as sister to *B. stolidia rubiginosa*. *Bistolida owenii*, a western Indian Ocean taxon, is sister to the Red Sea endemic *B. erythraeensis*. A new *Bistolida ursellus* sequence from the Andaman Sea is poorly supported as sister to the remaining *B. ursellus* taxon from the Pacific basin. Its placement is equally parsimonious as either sister to *B. ursellus* (Pacific) or forming a *B. ursellus* grade leading to the *B. kieneri* lineage. The topology of the two *B. ursellus* taxa as sisters is more likely and consistent with morphology.

One taxon is added to *Ovatipsa* and two taxa to *Talostolida*. Within *Ovatipsa*, the subspecies *O. chinensis amiges* from the Pacific basin and Western Australia is distinct from *O. chinensis chinensis* from the Philippines westward through the Indian Ocean to the east coast of Africa. Various other *O. chinensis* subspecies have been described within the Indian Ocean (e.g., Lorenz & Hubert, 1993), and preliminary data indicate that these Indian Ocean subspecies may represent very recent divergences within what I am currently recognizing as *O. chinensis chinensis*. However, until more individuals are sampled, I maintain them all under the taxon *Ovatipsa chinensis chinensis*. Within *Talostolida*, two taxa are added that appear as sisters to each other: *T. subteres* from southeastern Polynesia and *T. latior* from Hawaii. These two taxa are sister to *Talostolida pellucens*. All four taxa currently included within *Talostolida* are deeply divergent independent ESUs. A single haplotype of *Talostolida teres* "alveolus" (*sensu* Lorenz, 2002) is completely identical to haplotypes of *T. teres teres* individuals from both the Society Islands and the Tuamotu. Moreover, *T. teres* individuals from SE Polynesia have been described by Lorenz (2002) as a distinct subspecies *T. teres "janae"*; however sampled individuals of *T. teres* from SE Polynesia interfinger with individuals sampled from the Western Pacific (Papua New Guinea and Guam). Therefore, the data do not support *T. teres "janae"* as a valid taxon, based on my criteria. All Marquesan individuals sequenced possess *T. pellucens* haplotypes, whereas all *T. teres*-like individuals from the remainder of SE Polynesia possess *T. teres* haplotypes.

The *Cribrarula* clade includes eight additional taxa, making it the most diverse genus within Bistolidini. Two taxa, *Cribrarula taitae* from American Samoa and *C. garciai* from Easter Island, are added to the deeply divergent Pacific subclade. Both taxa are recently divergent members from their respective sister taxon. *Cribrarula taitae* appears as a closely related sister to *C. catholicorum*, and *C. garciai* is closely related to *C. cumingii*. Only a single individual from each of the two taxa was included in these analyses, and the results would be better addressed with multiple samples. Two members are added to the Western Indian Ocean subclade: *Cribrarula pellisserpentis* and *C. esontropia francescoi*, both from Madagascar. *Cribrarula esontropia francescoi* is a closely related sister to *C. esontropia esontropia*, which includes *C. esontropia cribellum* (Meyer, 2003). *Cribrarula pellisserpentis* is a deeply divergent member within the western Indian Ocean subclade and is sister to the other three ESUs. Four taxa are added to the remaining *Cribrarula* member clade. A single individual of *C. cribraria* from Masirah, Oman, appears significantly divergent from population samples of the previously unnamed *C. cribraria* ESU from the Andaman Sea. Conchologically, this individual approximates the western Indian Ocean taxon *C. cribraria abaliena* and is tentatively recognized as such. A single individual of *C. cribraria australiensis* from Western Australia falls within the Andaman *C. cribraria* cluster; therefore, I tentatively adopt the name *C. cribraria* cf. "*australiensis*" for a taxon that extends from the Andaman Sea southward to Western Australia. More exhaustive sampling is required to confirm these geographic patterns. A single individual of *C. exmouthensis magnifica* from Broome is significantly different from samples of *C. exmouthensis exmouthensis* from the Exmouth Gulf region, therefore validating the status of that taxon. Additional samples of *C. cribraria rotnnestensis* (N = 3) further validate the taxon's uniqueness. Eight individuals of *C. melwardi* from northeastern Australia all share a common ancestor and are reciprocally monophyletic with respect to the remaining *C. cribraria* individuals. Moreover, a single *C. cribraria cribraria* individual from the same reef (Lamont Reef in the Bunker Group) clusters as expected with other Pacific *C. cribraria cribraria* individuals. The final taxon included is *C. cribraria abrolhensis* (N = 3), and haplotypes are shallowly divergent but reciprocally monophyletic with respect to samples of *C. cribraria cribraria* (N = 30) from predominately western Pacific localities (Appendix). More thorough

analyses and discussion of this fascinating, species-rich group is in preparation (Meyer et al., in prep.).

#### Derived Compartment (Fig. 6)

The final compartment analyzed is the derived monophyletic clade recognized as the tribe Erroneini. This clade includes the following nine genera: *Austrasiatica*, *Pamulacypraea*, *Erronea*, *Purpuradusta*, *Contradusta*, *Notadusta*, *Eclogavena*, *Melicerona* and *Blasicrura*. Many (25) taxa are added within the tribe, and phylogenetic analyses result in some surprising affinities. For the most part, major genera are well supported, but their interrelationships are not. Three taxa currently ascribed to *Austrasiatica* were included in previous analyses (Meyer, 2003); however, they were considered as representatives of the genus *Nesiocypraea*. As discussed earlier, the finding that *Nesiocypraea teramachii* is distantly related raises the subgenus *Austrasiatica* to generic status for the clade that includes *Austrasiatica langfordi*, *A. hirasei* and *A. sakurai*. As in Meyer (2003), *Austrasiatica* is sister to all other Erroneini taxa, followed by *Pamulacypraea* as sister to the remainder. As predicted in Meyer (2003), the newly added *Pamulacypraea musumeeae* falls as sister to *P. katsuae*. Even with the addition of 24 taxa (a 67% increase), the topology among the rest of the major Erroneini lineages is ambiguous. Six added "*Erronea*" species form a basal grade leading to the *Adusta/Erronea* split previously recognized in Meyer (2003). I take a conservative approach and redefine *Erronea* to include all these taxa and subsume *Adusta* to a well-supported subclade within the group, as the new data demonstrate that *Adusta* and *Erronea* (including the more recent additions) are not equivalent (sisters). If *Adusta* were to be maintained at equivalent generic status, *Erronea* would represent a paraphyletic group. *Purpuradusta*, *Eclogavena*, *Melicerona* and *Blasicrura* are all well-supported monophyletic lineages. As in Meyer (2003), *Notadusta* is well supported only if restricted to members of the *Notadusta punctata* complex. However, because *Notadusta martini* is often considered a member of *Notadusta*, I include it within *Notadusta* here, although poorly supported. In a similarly conservative manner, I include two of the added taxa within *Contradusta*, although again poorly supported. Support for relationships among these seven genera is poor and is likely because of the short internode length between divergent lineages.

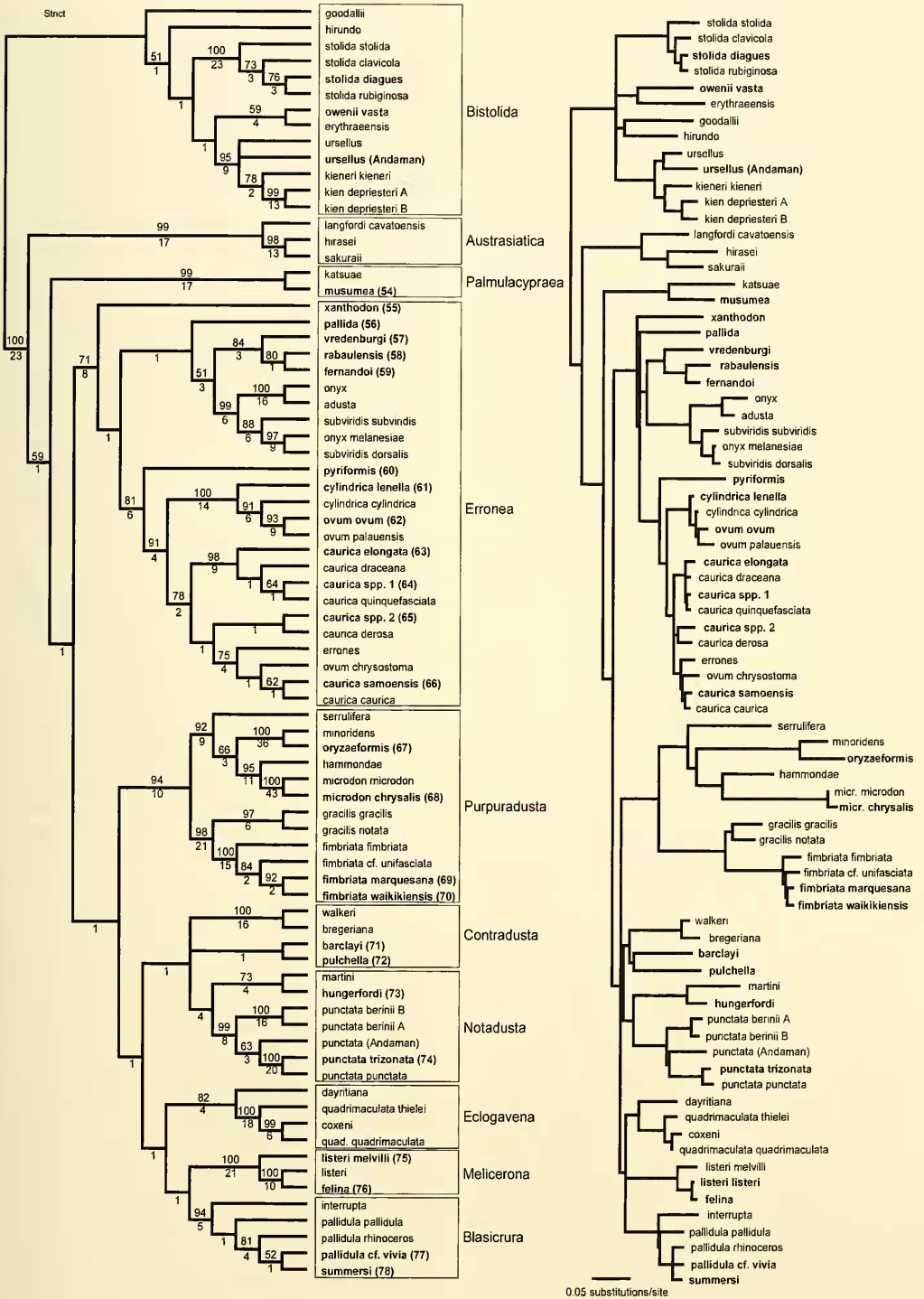


FIG. 6. Derived Compartment cladogram and phylogram. All other information as in Fig. 3.

Twelve additional taxa are added to *Erronea*. Six of the additions are traditionally recognized as distinct species, four have been recognized as subspecies, and two are newly discovered, but may have names associated with them that have been placed into synonymy. Of the new species, three form a relatively well-supported clade: *Erronea rabaulensis* shares a more recent common ancestor with *E. fernandoi* (80/1), and those two are sister to *E. vredenburgi* (84/3). The three additional *Erronea* species all nest deeply within the clade, and their relationships are not well supported. *Erronea pallida* appears as sister to the clade of the previously described three species and *Adusta*. *Erronea pyriformis* is relatively well supported (81/6) as the sister to the clade previously recognized as *Erronea* (Meyer, 2003). Finally, *Erronea xanthodon* falls at the base of *Erronea* and is sister to all other *Erronea* taxa. Within the crown *Erronea* subclade, six taxa are added that are all traditionally recognized at the subspecific level. Individuals of *Erronea cylindrica lenella* (N = 8, all from New Caledonia) form a monophyletic group strongly supported (91/6) as sister to the clade including the remaining *E. cylindrica* individuals plus two subspecies of *E. ovum*. These results imply that *E. cylindrica* at the specific level is a paraphyletic taxon. Newly added individuals of *Erronea ovum ovum* from both Singapore and the Philippines (N = 15) form a monophyletic group sister to *E. ovum palauensis* (N = 7). The four remaining, newly added taxa are all members of the *Erronea caurica* complex. First, individuals (N = 7) of the newly described *E. caurica samoensis* appear as a distinct lineage sister to individuals (N = 15) from the remainder of the Pacific and Western Australia (*E. caurica caurica*). Four geographically structured haplotype clades are found exclusively in the Western Indian Ocean. *Erronea caurica dracaena* is currently restricted to the Seychelles based on sampling. Newly added individuals from East Africa and Madagascar form a haplotype clade that I recognize as *Erronea caurica elongata*. Individuals of *E. caurica quinquefasciata* from the Red Sea, East Africa and Oman form the third monophyletic group. Finally, newly sequenced individuals from Masirah (N = 7) form a private haplotype clade (*E. caurica* ssp. #1) sister to *E. caurica quinquefasciata*. The final, newly added taxon (*E. caurica* ssp. #2) within the *E. caurica* complex is a clade (N = 18) that includes individuals primarily from India, but with a few individuals from Masirah, Oman. This haplotype clade is sister to the clade recognized previously as *E. caurica cf. derosa* from the

Andaman Sea (Meyer, 2003). The *Erronea caurica* complex and the associated *E. cylindrica*, *E. ovum* and *E. erronea* species will be more thoroughly addressed in another paper (Meyer, in prep.) as the group exhibits remarkable geographic structuring, polyphyly of recognized species (*E. ovum*), and evidence of introgression based on nuclear markers.

*Purpuradusta* is well supported and contains four newly added taxa that fall in expected relationships. The southeastern Polynesian endemic species *Purpuradusta oryzaeformis* is distinct and sister to *P. minoridens* that ranges throughout the remainder of the western IndoPacific. A single specimen of *P. microdon* from East Africa falls outside the haplotype clade of other sampled individuals from the Pacific basin (N = 5). This East African population is recognized as *Purpuradusta microdon chrysalis*. Two peripheral populations of *Purpuradusta fimbriata* in the Pacific Basin are introduced. First, Hawaiian populations of *P. fimbriata* are distinct (N = 7) and were previously recognized as *P. fimbriata waikikiensis*; thus this name is resurrected as a valid entity. Second, individuals from the Marquesas are also distinct genetically, consistent with the subspecies designation of Lorenz (2002), *P. fimbriata marquesana* (N = 14). Both of these Pacific *P. fimbriata* subclades share a more recent history with the widespread Pacific subspecies *P. fimbriata unifasciata*, as expected.

Two newly added species, "*Erronea*" *barclayi* and "*Erronea*" *pulchella*, come out as sister species in phylogenetic analyses. Moreover, these two taxa appear as sister to *Contradusta* in the most likely topology. Because of these results, and the poorly supported nature of their relationships, I tentatively place the two taxa in the genus *Contradusta*, with the caveat that they may be removed with future data. These results are somewhat surprising, particularly because "*Contradusta*" *pulchella* is thought to be closely related to *Erronea pyriformis* because of the darkly stained columellar dentition and overall conchological similarities. The sister relationship between *Contradusta pulchella* and *C. barclayi* is more acceptable as their divergence is deep, and the phylogenetic affiliations of *C. barclayi* were more difficult to predict based on morphological criteria. Another surprising result is the sister relationship between *Notadusta martini* and "*Erronea*" *hungerfordi*. Given these phylogenetic results, I tentatively place "*Erronea*" *hungerfordi* within *Notadusta*, but with little confidence, although it is reasonably supported (73/4), and suspect that it may be removed with more samples and



sequence data. Within the remaining *Notadusta* complex, individuals of *N. punctata trizonata* (N = 9) form a monophyletic group sister to the Pacific *N. punctata punctata* clade. Finally, in regards to *Notadusta*, "*Notadusta*" *rabaulensis* was mentioned previously as a member of *Erronea* and "*Notadusta*" *musumea* as *Palmulacypraea*, further reducing the membership of *Notadusta* (Meyer, 2003).

The final four additions to the dataset fall into *Melicerona* and *Blasicrura*. First, two taxa are added to *Melicerona*. Samples of *Melicerona listeri melvilli* (N = 5) from Queensland, Australia, form a monophyletic group sister to the remaining *Melicerona* taxa. (Two rostrate and melanistic individuals interfinger among the other three haplotypes indicating that the teratology is likely driven by phenotypic responses to environmental conditions rather than having a genetic basis.) Samples of *Melicerona felina* from both Oman and East Africa form a monophyletic group, and because the haplotypes from the two regions interfinger, there is no evidence for a distinction between the subspecies *M. felina felina* and *M. felina fabula*. Within *Blasicrura*, two taxa are added, based on the sequencing results. First, samples of *Blasicrura summersi*, a Fijian and Tonga endemic, appear as a recently divergent sister to the also newly included *B. pallidula* cf. *vivia* from American Samoa. This clade is sister to the Melanesian subspecies *Blasicrura pallidula rhinoceros*, as expected based on geography. This resulting topology indicates that the *Blasicrura pallidula* complex is paraphyletic.

## DISCUSSION

The ultimate goal of this project is to construct a comprehensive phylogeny of cypraeid gastropods at the appropriate level for diversification studies. From a molecular perspective, all ESUs presented are effectively equal units of diversity, whether they are currently recognized as species, subspecies or some other level. There are some noted exceptions as OTUs were used on occasion that represented unsorted or clinal variation within an ESU (e.g., *Erosaria miliaris/eburnea*). However, on a general scale, each taxon shown in the phylogenies (Figs. 3–6) represents an independent evolutionary trajectory.

Because so much taxonomic information is available for cowries, it is informative to see how molecular criteria compare with recognized taxonomic entities. The most recent compilation of the cowries is that of Lorenz (2002),

and I will use his checklist (pp. 250–291) as a benchmark for comparisons. Lorenz recognizes 232 species, of which I have sequenced 210 (> 90%), and they are presented herein. The missing species are as follows: *Nesiocypraea aenigma*, *N. lisetae*, *N. midwayensis*, *Austrasiatica alexhuberti*, *Erosaria ostergaardii*, *Zoila perlae*, *Lyncina camelopardis*, *L. joycae*, *Pustularia chiapponii*, *Cypraeovula colligata*, *C. cruickshanki*, *C. immelmani*, *Palmadusta androyensis*, *P. johnsonorum*, *Austrasiatica deforgesii*, *Palmulacypraea boucheti*, *P. omii*, *Eclogavena luchuana*, *Erronea* (?) *angioyorum*, and *E. nymphae*. Sequences from samples of both *Purpuradusta barbieri* and "*Talostolida*" *rashleighana* have been obtained, but were too late for inclusion in these analyses. All missing species are rare, with small ranges located generally at the periphery of their putative sister species based on conchological and anatomical characters. Of the 210 sequenced species, phylogenetic comparisons and molecular criteria support all but 15 (93%) as ESUs. The 15 recognized species not supported by my criteria are discussed below. For *Nucleolaria granulata*, *Monetaria obvelata*, *Erosaria eburnea*, *Zoila orientalis*, *Z. thersites*, *Luria controversa*, *L. gilvella*, *Notocypraea occidentalis*, and *Palmadusta humphreysii*, multiple individuals were sequenced and the haplotypes interfingered within their closest relative. For the next six species that I do not support, only a single individual was sequenced, thus they may indeed represent a very young independent trajectory. However, when compared to the genetic diversity within their closest relative, the genetic difference is unremarkable, and in some instances, only a single mutation different from putative conspecifics: *Zonaria angelicae*, *Z. petitiana*, *Cypraeovula mikeharti*, *Bistolida brevidentata*, *Cribrarula garciai*, and *C. taitae*.

While genetic data are overall broadly consistent with taxa recognized at the specific level, the results are even more remarkable when compared among taxa recognized at subspecific levels. Lorenz recognizes 260 taxa at the subspecific level. Of those 260 subspecies, I have sequenced at least two individuals from 160 in order to assess their validity. Molecular criteria support 113 (> 70%) of these taxa as legitimate ESUs. Moreover, sequence results indicate an additional 20 distinct ESUs not recognized as subspecies by Lorenz (but sometimes mentioned as important varieties or forms). A full listing of sampled taxa and their current ESU status as indicated by the prior criteria can be found at the Cowrie Ge-

netic Database Project Website (<http://www.flmnh.ufl.edu/cowries>). The website includes other information, such as localities sampled, numbers of individuals for each taxon, and photographs of the specimens sequenced.

Overwhelming molecular support for traditionally recognized taxa, both at specific and sub-specific levels, is extremely encouraging. First, from a taxonomic standpoint, these molecular results corroborate the excellent work done by centuries of malacological researchers, at both professional and amateur levels. Similar molecular surveys of other diverse groups will provide valuable comparisons in order to assess taxonomic congruence (e.g., Jackson & Cheetham, 1990) and address concordant diversification patterns. Second, from a molecular perspective, sequence data provide a suitable, objective, relative metric for circumscribing appropriate evolutionary units. Assuming rate constancy in the molecules (COI only, in prep.), molecular divergences can constrain the tempo of diversification and assess the distinctiveness of purported taxa. A growing body of molecular data across the diversity of life undoubtedly will provide insight to some of our most fundamental evolutionary questions.

#### ACKNOWLEDGEMENTS

An ever-growing number of individual and institutions have contributed and supported this ongoing research. Without their assistance, the work would not be possible. The following persons are recognized: Nonoy Alonzo, Vicente Azurin, Paul Barber, Don Barclay, Marty Beals, Victor Bonito, Philippe Bouchet, Michel Boutet, Roy Caldwell, Carlos Carvalho, Hank Chaney, John Chester, Peter Clarkson, Lori Bell Colin, Pat Colin, Allen Collins, Harry Conley, Vince Crayssac, Carolyn Cruz, Donald Dan, Martyn Day, Bruno de Bruin, Helen deJode, John Earle, Andrew Edinger, Mark Erdmann, Melissa Frey, Michel Garcia, Bill Gibbs, Serge Gofas, Terry Gosliner, Jeroen Goud, Robert Gourguet, Fabien Goutal, Paulo Granja, Kibata Mussa Haji, Jerry Harasewych, Itaru Hayami, Brian Hayes, Claus Hedegaard, Ed Heiman, Bert Hoeksema, John Hoover, John Jackson, Maurice Jay, Scott Johnson, Paul Kanner, Yasunori Kano, Tomoki Kase, Norbert Kayombo, Shigemitsu Kinjo, Lisa Kirkendale, Kitona Kombo Kitona, Utih Kukun, Senthil Kumar, Jean Paul Lefort, Bill Liltved, Hung-Chang Liu, Charlotte Lloyd, Felix Lorenz, Jr., Felix Lorenz, Sr., Larry Madrigal, Marlene Martinez, Gerald McCormack, Mohammed Mohammed, Hugh Morrison, Gowele Mtoka,

Mtumwa Mwadini, Peter Ng, Steve Norby, Shuichi Ohashi, Yoshihiro Omi, Ina Park, Marcel Pin, Cory Pittman, Xavier Pochon, Matt Richmond, Raphael Ritson-Williams, Gonçalo Rosa, Gary Rosenberg, Teina Rongo, Fred Schroeder, Mike Severns, Pauline Severns, Hung-Long Shi, Brian Simison, Michael Small, John Starmer, Steve Tettlebach, David Touitou, Martin Wallace, Chia-Hsiang Wang, Dave Watts, Barry Wilson, Woody Woodman, Shu-Ho Wu. The following institutions are acknowledged: Florida Museum of Natural History; University of California Museum of Paleontology; Academy of Natural Sciences of Philadelphia; Bernice P. Bishop Museum, Honolulu, Hawaii; California Academy of Sciences; Institute of Marine Sciences, Zanzibar; University of Dar es Salaam; Jacksonville Shell Club; Musée National d'Histoire Naturelle, Paris, France; National Museum of Natural History Naturalis, Leiden, The Netherlands; Santa Barbara Museum of Natural History; National Museum of Natural History; and Suganthi Devadason Marine Research Institute. I also would like to thank Felix Lorenz, Jr., for his thoughtful comments, as well as the reviews of four anonymous reviewers. Final decisions and opinions are wholly mine.

This research has been financially supported by the following NSF grants: DEB-9807316, DEB 0196049, and OCE-0221382.

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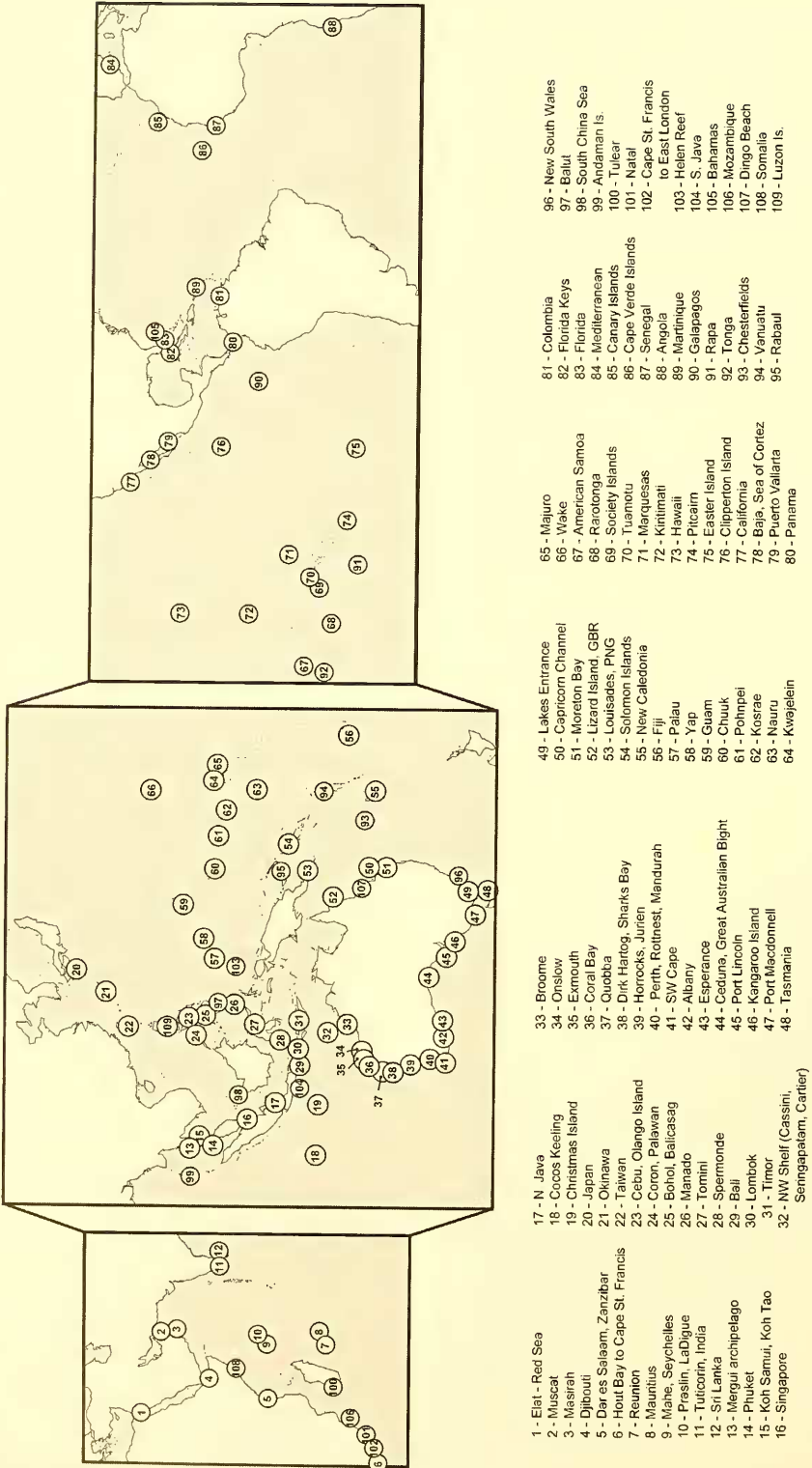


FIG. 7. Sampled localities indicated for listed taxa in Appendix (column 3).

APPENDIX 1: Sampled Taxa and Supplementary Data

New taxa and sequence data are numbered and bolded. Additional, newly sampled localities for taxa previously reported are also bolded. Crossouts are names previously used in Meyer (2003) that are corrected herein because of taxonomic revisions. \*for the legend see Fig. 7.

OTUs	Authors	Sampled localities*	Accession #	
			16S	COI
OUTGROUPS				
<i>Jenneria pustulata</i>	Lightfoot, 1786	79	AY161402	AY161635
<i>Pseudocypraea adamsonii</i>	Sowerby I, 1832	5	AY161403	AY161636
<b>1. <i>Pseudocypraea exquiusita</i></b>	<b>Petuch, 1979</b>	<b>23</b>	<b>AY534351</b>	<b>AY534428</b>
<i>Pedicularia pacifica</i>	Pease, 1865	57, <b>59</b>	AY161384	AY161617
<i>Crenavolva tokuoi</i>	Azuma, 1989	25	AY161390	AY161623
<i>Prionovolva brevis</i>	Sowerby I, 1828	23	AY161391	AY161624
<i>Serratovolva dondani</i>	Cate, 1964	23	AY161392	AY161625
<i>Phenacovolva tokioi</i>	Cate, 1973	26	AY161393	AY161626
<i>Crenavolva cf rosewateri</i>	Cate, 1973	25	AY161394	AY161627
<b>2. <i>Volva volva</i></b>	<b>Linnaeus, 1758</b>	<b>22</b>	<b>AY534352</b>	<b>AY534429</b>
<i>Phenacovolva weaveri</i>	Cate, 1973	25	AY161395	AY161628
<b>3. <i>Primovula concinna</i></b>	<b>Adams &amp; Reeve, 1848</b>	<b>5</b>	<b>AY534353</b>	<b>AY534430</b>
<b>4. <i>Dentiovula takeoi</i></b>	<b>Cate &amp; Azuma, 1973</b>	<b>57</b>	<b>AY534354</b>	<b>AY534431</b>
<b>5. <i>Prosimnia semperi</i></b>	<b>Weinkauff, 1881</b>	<b>57</b>	<b>AY534355</b>	<b>AY534432</b>
<i>Adamantia florida</i>	Kuroda, 1958	25	AY161396	AY161629
<i>Calpurnus verrucosus</i>	Linnaeus, 1758	30	AY161397	AY161630
<i>Calpurnus lacteus</i>	Lamarck, 1810	59	AY161398	AY161631
<i>Ovula ovum</i>	Linnaeus, 1758	28	AY161399	AY161632
<i>Cyphoma gibbosum</i>	Linnaeus, 1758	83	AY161400	AY161633
<i>Simnia aequalis</i>	Sowerby I, 1832	78	AY161401	AY161634

(continues)

OTUS	Authors	Sampled localities*	Accession #	
			16S	COI
INGROUPS				
6. <i>Propustularia surinamensis</i>	Perry, 1811	89	AY534356	AY534433
7. <i>Nesiocypraea teramachii neocaledonica</i>	Lorenz, 2002	93	AY534357	AY534434
<i>Ipsa childreii</i>	Gray, 1825	59, 64	AY161404	AY161637
<i>Cryptocypraea dillwynii</i>	Schilder, 1922	59	AY161411	AY161644
<i>Nucleolaria nucleus</i>	Linnaeus, 1758	5, 53, 64, 69	AY161417	AY161650
<i>Nucleolaria granulata</i>	Pease, 1862	73	AY161418	AY161651
<i>Staphylaea limacina interstincta</i>	Wood, 1828	5, 9	AY161412	AY161645
<i>Staphylaea limacina limacina</i>	Lamarck, 1810	23, 30, 51	AY161413	AY161646
<i>Staphylaea staphylaea laevigata</i>	Dautzenberg, 1932	5, 8	AY161414	AY161647
<i>Staphylaea staphylaea staphylaea</i>	Linnaeus, 1758	20, 51, 52, 53, 59	AY161415	AY161648
<i>Staphylaea semiplota</i>	Mighels, 1845	73	AY161416	AY161649
<i>Monetaria annulus</i>	Linnaeus, 1758	3, 5, 8, 10, 30, 52, 68	AY161405	AY161638
<i>Monetaria obvelata</i>	Lamarck, 1810	68, 69, 70	AY161406	AY161639
<i>Monetaria moneta</i>	Linnaeus, 1758	5, 8, 30, 71, 59	AY161407	AY161640
<i>Monetaria caputserpentis caputophidii</i>	Schilder, 1927	73	AY161409	AY161642
<i>Monetaria caputserpentis caputserpentis</i>	Linnaeus, 1758	5, 19, 59, 66, 71, 91	AY161408	AY161641
<i>Monetaria caputserpentis</i>	Melville, 1888	75	AY161410	AY161643
<i>Perisserosa guttata</i>	Gmelin, 1791	25	AY161419	AY161652
8. <i>Erosaria marginalis</i>	Dillwyn, 1827	5, 108	AY534358	AY534435
9. <i>Erosaria citrina</i>	Gray, 1825	100, 101	AY534359	AY534436
<i>Erosaria helvola helvola</i>	Linnaeus, 1758	5, 10, 30, 53, 59, 69, 70	AY161429	AY161662
<i>Erosaria helvola hawaiiensis</i>	Melville, 1888	73	AY161430	AY161663
10. <i>Erosaria helvola cf. callista</i>	Shaw, 1909	71	AY534360	AY534437
<i>Erosaria turdus</i>	Lamarck, 1810	1, 2	AY161420	AY161653
11. <i>Erosaria irrorata</i>	Gray, 1828	69, 70	AY534361	AY534438
<i>Erosaria albuginosa</i>	Gray, 1825	79	AY161427	AY161660
<i>Erosaria poraria</i>	Linnaeus, 1758	19, 59, 69	AY161428	AY161661
<i>Erosaria beckii</i>	Gaskoin, 1836	59, 23, 31	AY161425	AY161658
12. <i>Erosaria macandrewi</i>	Sowerby II, 1870	1	AY534362	AY534439
13. <i>Erosaria engleri</i>	Summers & Burgess, 1965	75	AY534363	AY534440

(continues)

(continued)

OTUS	Authors	Sampled localities*	Accession #	
			16S	COI
<i>Erosaria kingae</i>	Rehder & Wilson, 1975	74	AY161424	AY161657
<i>Erosaria thomasi</i>	Crosse, 1865	71	AY161426	AY161659
<i>Erosaria cernica</i>	Sowerby II, 1870	38, 73	AY161423	AY161656
<i>Erosaria spurca</i>	Linnaeus, 1758	84, 85, 86	AY161421	AY161654
<i>Erosaria acicularis</i>	Gmelin, 1791	83	AY161422	AY161655
<i>Erosaria labrolineata</i>	Gaskoin, 1849	52, 25	AY161433	AY161666
<i>Erosaria boivini</i>	Kiener, 1843	20, 23	AY161434	AY161667
<i>Erosaria ocellata</i>	Linnaeus, 1758	2, 12	AY161431	AY161664
<i>Erosaria gangranosa</i>	Dillwyn, 1817	14	AY161432	AY161665
<i>Erosaria lamarckii cf. redimita</i>	Melville, 1888	14	AY161437	AY161670
<b>14. <i>Erosaria lamarckii lamarckii</i></b>	<b>Gray, 1825</b>	<b>5</b>	<b>AY534364</b>	<b>AY534441</b>
<i>Erosaria millaris</i>	Gmelin, 1791	15, 33	AY161435	AY161668
<i>Erosaria eburnea</i>	Barnes, 1824	54, 55	AY161436	AY161669
<i>Erosaria nebrites</i>	Melville, 1888	1, 2	AY161438	AY161671
<i>Erosaria erosa</i> (Indian)	Linnaeus, 1758	5, 8, 10, 14	AY161440	AY161673
<i>Erosaria erosa</i> (Pacific) <i>cf. chlorizans</i>	Melville, 1888	19, 30, 59, 69	AY161439	AY161672
<i>Umbilia armeniaca</i>	Verco, 1912	43, 44, 45	AY161493	AY161726
<i>Umbilia hesitata</i>	Iredale, 1916	48, 49	AY161492	AY161725
<i>Umbilia capricornica</i>	Lorenz, 1989	50	AY161494	AY161727
<b>15. <i>Umbilia cf. petillirostris</i></b>	<b>Darragh, 2002</b>	<b>50</b>	<b>AY534365</b>	<b>AY534442</b>
<i>Macrocypraea cervinetta</i>	Kiener, 1843	79	AY161485	AY161718
<i>Macrocypraea cenus</i>	Linnaeus, 1771	83, 82	AY161486	AY161719
<i>Macrocypraea zebra</i>	Linnaeus, 1758	82, 83	AY161487	AY161720
<i>Leporicypraea valentia</i>	Perry, 1811	25	AY161484	AY161717
<i>Leporicypraea mappa rosea</i>	Gray, 1824	8	AY161480	AY161713
<b>16. <i>Leporicypraea mappa aiwalensis</i></b>	<b>Lorenz, 2002</b>	<b>101</b>	<b>AY534366</b>	<b>AY534443</b>
<i>Leporicypraea mappa mappa</i>	Linnaeus, 1758	22, 23, 98	AY161481	AY161714
<i>Leporicypraea geographica</i>	Schilder & Schilder, 1933	5, 10, 14, 32, 54, 56, 57, 98	AY161482	AY161715
<i>Leporicypraea mappa penneryana-viridis</i>	Melville, 1888; Kenyon, 1902	55, 57, 59, 64	AY161479	AY161712
<i>Leporicypraea mappa penneryana-viridis admirabilis</i>	Kenyon, 1902; Lorenz, 2002	71	AY161483	AY161716
<i>Mauritia scurra indica</i>	Gmelin, 1791	30, 59, 71	AY161477	AY161710
<i>Mauritia scurra scurra</i>	Gmelin, 1791	5, 10	AY161478	AY161711

(continues)

(continued)

OTUS	Authors	Sampled localities*	Accession #	
			16S	COI
<i>Mauritia mauritiana</i>	Linnaeus, 1758	5, 19, 52, 70	AY161474	AY161707
<i>Mauritia depressa dispersa</i>	Schilder & Schilder, 1939	10, 19	AY161475	AY161708
<i>Mauritia depressa depressa</i>	Gray, 1824	59, 64, 69	AY161476	AY161709
<i>Mauritia grayana</i>	Schilder, 1930	2, 3	AY161467	AY161700
<i>Mauritia eglanina</i>	Dulcos, 1833	32, 52, 59, 64	AY161469	AY161702
<i>Mauritia histrio</i>	Gmelin, 1791	5, 9, 19	AY161470	AY161703
<i>Mauritia arabica arabica</i>	Linnaeus, 1758	19, 21, 22, 23, 25, 29, 30, 32, 33, 52, 55, 56, 59, 61, 63, 64	AY161465	AY161698
<b>17. <i>Mauritia arabica arabica</i> (Am. Samoa)</b>		<b>67</b>	<b>AY534367</b>	<b>AY534444</b>
<i>Mauritia arabica asiatica</i>	Schilder & Schilder, 1939	2, 11, 13, 15, 19, 23, 29, 30	AY161466	AY161699
<i>Mauritia arabica immanis</i>		5, 7, 8	AY161468	AY161701
<i>Mauritia maculifera</i> (Marquesas) <i>martybealsi</i>	Lorenz, 2002	71	AY161472	AY161705
<i>Mauritia maculifera</i> (N. Pacific) <i>maculifera</i>	Schilder, 1932	59, 66, 73	AY161471	AY161704
<i>Mauritia maculifera</i> (Polynesia) <i>scindata</i>	Lorenz, 2002	69, 70	AY161473	AY161706
<b>18. <i>Barycypraea teulerei</i></b>	<b>Cazenavette, 1846</b>	<b>3</b>	<b>AY534368</b>	<b>AY534445</b>
<b>19. <i>Barycypraea fultoni</i></b>	<b>Sowerby III, 1903</b>	<b>106</b>	<b>AY534369</b>	<b>AY534446</b>
<i>Zoila marginata marginata</i>	Gaskoin, 1849	43, 44, 45, 46	AY161495	AY161728
<b>20. <i>Zoila marginata ketyana</i></b>	<b>Raybaudi, 1978</b>	<b>38, 39, 40</b>	<b>AY534370</b>	<b>AY534447</b>
<i>Zoila rosselli</i>	Cotton, 1948	37, 38, 39, 40, 41, 42, 43	AY161497	AY161730
<i>Zoila venusta</i>	Sowerby II, 1846	39, 40, 41, 43	AY161496	AY161729
<i>Zoila eludens</i>	Raybaudi, 1991	35	AY161499	AY161732
<i>Zoila decipiens</i>	Smith, 1880	33, 34	AY161498	AY161731
<b>21. <i>Zoila mariellae</i></b>	<b>Raybaudi, 1983</b>	<b>32 (?)</b>	<b>AY534371</b>	<b>AY534448</b>
<i>Zoila thersites</i>	Gaskoin, 1849	45, 46	AY161503	AY161736
<i>Zoila jeaniana sherylae</i>	Raybaudi, 1990	37	AY161500	AY161733
<i>Zoila jeaniana jeaniana</i>	Cate, 1968	36	AY161501	AY161734
<i>Zoila friendii friendii</i>	Gray, 1831	39, 40, 41, 42, 43	AY161502	AY161735
<i>Muracypraea mus</i>	Linnaeus, 1758	81	AY161491	AY161724
<i>Cypraea tigris</i> (Indian)	Linnaeus, 1758	3, 5, 8, 9, 10, 14	AY161489	AY161722
<i>Cypraea tigris</i> (Pacific)		15, 18, 19, 23, 30, 32, 33, 52, 56, 57, 59, 60, 61, 62, 63, 64, 69, 70, 73	AY161488	AY161721
<i>Cypraea pantherina</i>	Lightfoot, 1786	1	AY161490	AY161723

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OTUS	Authors	Sampled localities*	Accession #	
			16S	COI
<i>Talparia talpa</i>	Linnaeus, 1758	5, 30, 64	AY161464	AY161697
<b>22. <i>Talparia exusta</i></b>	<b>Sowerby I, 1832</b>	<b>4</b>	<b>AY534372</b>	<b>AY534449</b>
<i>Luria lurida</i>	Linnaeus, 1758	84, 86, 87	AY161462	AY161695
<i>Luria cinerea</i>	Gmelin, 1791	83, <b>82</b> , <b>105</b>	AY161461	AY161694
<i>Luria pulchra</i>	Gray, 1824	2	AY161463	AY161696
<i>Luria tessellata</i>	Swainson, 1822	73	AY161460	AY161693
<i>Luria isabella</i>	Linnaeus, 1758	5, 8, 9, 20, 30, 65, 69, 73, <b>98</b>	AY161458	AY161691
<i>Luria isabellamexicana</i>	Stearns, 1893	76, 79	AY161459	AY161692
<i>Annepona mariae</i>	Schilder, 1927	59, 64, 70	AY161443	AY161676
<i>Trona stercoraria</i>	Linnaeus, 1758	87	AY161441	AY161674
<i>Chelycypraea testudinaria</i>	Linnaeus, 1758	5, 59, 64	AY161442	AY161675
<i>Lyncina (Austrocypraea) reevei</i>	Sowerby I, 1832	41, 45	AY161444	AY161677
<i>Lyncina (cf. Miolyncina) porteri</i>	Cate, 1966	97	AY161448	AY161681
<i>Lyncina (Arestoides) argus argus</i>	Linnaeus, 1758	30, 59	AY161445	AY161678
<b>23. <i>Lyncina (Arestoides) argus</i></b> <b>contrastrinata</b>	<b>Perry, 1811</b>	<b>10</b>	<b>AY534373</b>	<b>AY534450</b>
<b>24. <i>Lyncina (Callistocypraea) broderipii</i></b>	<b>Sowerby I, 1832</b>	<b>101</b>	<b>AY534374</b>	<b>AY534451</b>
<i>Lyncina (Callistocypraea) nivosa</i>	Broderip, 1827	13, 14	AY161446	AY161679
<i>Lyncina (Callistocypraea) leucodon</i>	Broderip, 1827	23, <b>57</b>	AY161447	AY161680
<i>Lyncina (Callistocypraea) aurantium</i>	Gmelin, 1791	59, <b>54</b>	AY161449	AY161682
<i>Lyncina ventriculus</i>	Lamarck, 1810	59, 69, 70	AY161452	AY161685
<b>25. <i>Lyncina ventriculus (Xmas IO)</i></b>		<b>19</b>	<b>AY534375</b>	<b>AY534452</b>
<i>Lyncina sulcidentata</i>	Gray, 1824	73	AY161450	AY161683
<b>26. <i>Lyncina kuroharai</i></b>	<b>Kuroda &amp; Habe, 1961</b>	<b>20</b>	<b>AY534376</b>	<b>AY534453</b>
<i>Lyncina schilderorum</i>	Iredale, 1939	69, 70, 73	AY161451	AY161684
<i>Lyncina lynx</i>	Linnaeus, 1758	9, 30, 69, <b>5</b>	AY161456	AY161689
<i>Lyncina vitellus</i>	Linnaeus, 1758	5, 8, 30	AY161457	AY161690
<i>Lyncina leviathan</i>	Schilder & Schilder, 1937	5, 20, 55, 59, 69, 73	AY161453	AY161686
<i>Lyncina carneola</i>	Linnaeus, 1758	1, 9, 13, 20, 30, 52, 53, 55, 59, 69	AY161454	AY161687
<i>Lyncina propinqua</i>	Garrett, 1879	69, 71	AY161455	AY161688
<i>Pustularia globulus globulus</i>	Linnaeus, 1758	59	AY161507	AY161740
<i>Pustularia globulus brevirostris</i>	Schilder & Schilder, 1938	5, 10	AY161508	AY161741

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OTUS	Authors	Sampled localities*	Accession #	
			16S	COI
<i>Pustularia bistrinotata bistrinotata</i>	Schilder & Schilder, 1937	27, 59, 64	AY161504	AY161737
<b>27. <i>Pustularia bistrinotata keelingensis</i></b>	<b>Schilder &amp; Schilder, 1940</b>	<b>98</b>	<b>AY534377</b>	<b>AY534454</b>
<b>28. <i>Pustularia bistrinotata sublaevis</i></b>	<b>Schilder &amp; Schilder, 1938</b>	<b>69, 70</b>	<b>AY534378</b>	<b>AY534455</b>
<i>Pustularia mauiensis</i>	Burgess, 1967	73	AY161505	AY161738
<i>Pustularia cicercula</i>	Linnaeus, 1758	5, 14, 59, 64, 69	AY161506	AY161739
<i>Pustularia margarita</i>	Dillwyn, 1817	59	AY161509	AY161742
<i>Neobernaya spadicea</i>	Swainson, 1823	77	AY161517	AY161750
<i>Pseudozonaria annettae</i>	Dall, 1909	78	AY161518	AY161751
<i>Pseudozonaria arabicula</i>	Lamarck, 1810	79	AY161519	AY161752
<b>29. <i>Pseudozonaria nigropunctata</i></b>	<b>Gray, 1828</b>	<b>90</b>	<b>AY534379</b>	<b>AY534456</b>
<i>Pseudozonaria robertsi</i>	Hidalgo, 1906	80	AY161520	AY161753
<b>30. <i>Schilderia achatidea</i></b>	<b>Sowerby I, 1837</b>	<b>84</b>	<b>AY534380</b>	<b>AY534457</b>
<i>Zonaria sanguinolenta</i>	Gmelin, 1791	87	AY161512	AY161745
<b>31. <i>Zonaria picta</i></b>	<b>Gray, 1824</b>	<b>86</b>	<b>AY534381</b>	<b>AY534458</b>
<i>Zonaria zonaria</i>	Gmelin, 1791	87	AY161513	AY161746
<i>Zonaria pyrum senegalensis</i>	Schilder, 1928	87	AY161510	AY161743
<i>Zonaria pyrum angolensis</i>	Odhner, 1923	88	AY161511	AY161744
<b>32. <i>Zonaria pyrum angelicae</i></b>	<b>Clover, 1974</b>	<b>87</b>	<b>AY534382</b>	<b>AY534459</b>
<b>33. <i>Notocypraea hartsmithi</i></b>	<b>Schilder, 1967</b>	<b>96</b>	<b>AY534383</b>	<b>AY534460</b>
<i>Notocypraea piperita</i>	Gray, 1847	41, 43, 45, 48	AY161524	AY161757
<i>Notocypraea pulicaria</i>	Reeve, 1846	41	AY161525	AY161758
<i>Notocypraea comptoni</i>	Gray, 1847	43, 45, 47, 48, 49	AY161521	AY161754
<i>Notocypraea angustata</i>	Gmelin, 1791	47, 48	AY161522	AY161755
<b>34. <i>Notocypraea angustata</i> (Port Lincoln)</b>		<b>45</b>	<b>AY534384</b>	<b>AY534461</b>
<i>Notocypraea declivis</i>	Sowerby II, 1870	47, 48	AY161523	AY161756
<i>Cypraeovula connelli</i>	Littved, 1983	102	AY161527	AY161760
<i>Cypraeovula castanea</i>	Higgins, 1868	6	AY161526	AY161759
<i>Cypraeovula iutsumi</i>	Shikama, 1974	102	AY161528	AY161761
<i>Cypraeovula capensis</i>	Gray, 1828	102	AY161530	AY161763
<b>35. <i>Cypraeovula fuscovulva</i></b>	<b>Shaw, 1909</b>	<b>6</b>	<b>AY534385</b>	<b>AY534462</b>
<b>36. <i>Cypraeovula fuscodentata</i></b>	<b>Gray, 1825</b>	<b>6</b>	<b>AY534386</b>	<b>AY534463</b>
<i>Cypraeovula coronata</i>	Schilder, 1930	102	AY161529	AY161762

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OTUs	Authors	Sampled localities*	Accession #	
			16S	COI
37. <i>Cypraeovula mikeharti</i>	Lorenz, 1985	6	AY534387	AY534464
38. <i>Cypraeovula algoensis</i>	Gray, 1825	6	AY534388	AY534465
<i>Cypraeovula edentula</i>	Gray, 1825	102	AY161531	AY161764
<i>Cypraeovula alfredensis</i>	Schilder & Schilder, 1929	102	AY161532	AY161765
<i>Palmadusta contaminata distans</i>	Schilder & Schilder, 1938	5	AY161555	AY161789
<i>Palmadusta contaminata contaminata</i>	Sowerby I, 1832	25, 32, 71	AY161556	AY161790
<i>Palmadusta asellus cf. bitaeniata</i>	Geret, 1903	30, 63	AY161543	AY161777
<i>Palmadusta asellus cf. asellus</i>	Linnaeus, 1758	5	AY161545	AY161779
<i>Palmadusta asellus cf. vespacea</i>	Melvill, 1905	10, 23, 25	AY161544	AY161778
<i>Palmadusta saulae</i>	Gaskoin, 1843	13, 20	AY161554	AY161788
<i>Palmadusta lentiginosa</i>	Gray, 1825	3, 11	AY161557	AY161791
<i>Palmadusta humphreysii</i>	Gray, 1825	55, 51	AY161550	AY161784
<i>Palmadusta lutea</i>	Gmelin, 1791	23, 64	AY161549	AY161783
<i>Palmadusta ziczac ziczac</i>	Linnaeus, 1758	25, 54	AY161552	AY161786
<i>Palmadusta ziczac misella</i>	Perry, 1811	5	AY161553	AY161787
<i>Palmadusta diluculum</i>	Reeve, 1845	5, 10	AY161558	AY161792
<i>Palmadusta clandestina passerina</i>	Melvill, 1888	3, 5, 10, 8	AY161548	AY161782
39. <i>Palmadusta clandestina cf. clandestina</i> (Andaman)	Linnaeus, 1758	14	AY534389	AY534466
<i>Palmadusta artuffeli</i>	Jousseume, 1876	20	AY161546	AY161780
<i>Palmadusta clandestina elandestina cf. candida</i>	Pease, 1865	23, 30, 33, 38, 53, 55, 59, 64, 28	AY161547	AY161781
<i>Bistolida stolidia stolidia</i>	Linnaeus, 1758	24, 32, 55, 59, 23, 51, 64	AY161536	AY161770
<i>Bistolida stolidia clavicola</i>	Melvill, 1888	5	AY161534	AY161768
40. <i>Bistolida stolidia diagues</i>	Melvill, 1888	10	AY534390	AY534467
<i>Bistolida stolidia rubiginosa</i>	Gmelin, 1791	30	AY161535	AY161769
<i>Bistolida erythraeensis</i>	Sowerby I, 1837	4	AY161533	AY161767
41. <i>Bistolida owenii</i>	Sowerby I, 1837	100	AY534391	AY534468
<i>Bistolida goodallii</i>	Sowerby I, 1832	69, 72	AY161537	AY161771
<i>Bistolida hiruudo</i>	Linnaeus, 1758	14, 15, 52, 53, 55, 59, 12	AY161539	AY161773
<i>Bistolida ursellus</i>	Gmelin, 1791	25, 59	AY161541	AY161775
42. <i>Bistolida ursellus</i> (Andaman)		14	AY534392	AY534469

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OTUs	Authors	Sampled localities*	Accession #	
			16S	COI
<i>Bistolida kieneri kieneri</i>	Hidalgo, 1906	5, 8, 9	AY161542	AY161776
<i>Bistolida kieneri depriesteri</i> A	Schilder, 1933	29, 52	AY161540	AY161774
<i>Bistolida kieneri depriesteri</i> B		19, 28, 29	AY161538	AY161772
<i>Ovatipsa chinensis chinensis</i>	Gmelin, 1791	5, <b>25, 29</b>	AY161559	AY161793
<b>43. <i>Ovatipsa chinensis amiges</i></b>	<b>Melville &amp; Standen, 1904</b>	<b>38, 53, 59, 73, 23</b>	<b>AY534393</b>	<b>AY534470</b>
<i>Ovatipsa coloba</i>	Melville, 1888	14, 3	AY161560	AY161794
<i>Talostolida teres</i>	Gmelin, 1791	53, 59, 69, <b>98</b>	AY161561	AY161795
<i>Talostolida pellucens</i>	Melville, 1888	5, 14, 19, 30, 38, 59, 64, 73, 76, 80, <b>71</b>	AY161562	AY161796
<b>44. <i>Talostolida subteres</i></b>	<b>Weinkauff, 1881</b>	<b>70</b>	<b>AY534394</b>	<b>AY534471</b>
<b>45. <i>Talostolida latior</i></b>	<b>Melville, 1888</b>	<b>73</b>	<b>AY534395</b>	<b>AY534472</b>
<i>Cribrarula gaskoini</i>	Reeve, 1846	73	AY161572	AY161806
<i>Cribrarula catholicorum</i>	Schilder & Schilder, 1938	54	AY161575	AY161809
<b>46. <i>Cribrarula taitae</i></b>	<b>Burgess, 1993</b>	<b>67</b>	<b>AY534396</b>	<b>AY534473</b>
<i>Cribrarula cumingii</i>	Sowerby I, 1832	69, 70	AY161573	AY161807
<b>47. <i>Cribrarula garciai</i></b>	<b>Lorenz &amp; Raines, 2001</b>	<b>75</b>	<b>AY534474</b>	<b>AY534474</b>
<i>Cribrarula astaryi</i>	Schilder, 1971	71	AY161574	AY161808
<i>Cribrarula cribraria comma</i>	Perry, 1811	5	AY161565	AY161799
<b>48. <i>Cribrarula pellisserpentis</i></b>	<b>Lorenz, 1999</b>	<b>100</b>	<b>AY534397</b>	<b>AY534475</b>
<b>49. <i>Cribrarula esontropia francescoi</i></b>	<b>Lorenz, 2002</b>	<b>100</b>	<b>AY534398</b>	<b>AY534476</b>
<i>Cribrarula cribellum</i>	Gaskoin, 1849	7	AY161563	AY161797
<i>Cribrarula esontropia</i>	Duclos, 1833	7	AY161564	AY161798
<i>Cribrarula fallax</i>	Smith, 1881	41	AY161569	AY161803
<i>Cribrarula cribraria (Andaman) australiensis</i>	<b>Lorenz, 2002</b>	<b>14, 38</b>	<b>AY161567</b>	<b>AY161801</b>
<b>50. <i>Cribrarula cribraria cf. abaliena</i></b>	<b>Lorenz, 1989</b>	<b>3</b>	<b>AY534399</b>	<b>AY534477</b>
<i>Cribrarula gaspari</i>	Biraghi, & Nicolay, 1993	64	AY161570	AY161804
<i>Cribrarula erbrattia-exmouthensis</i>	Melville, 1888	35	AY161571	AY161805
<b>51. <i>Cribrarula exmouthensis magnifica</i></b>	<b>Lorenz, 2002</b>	<b>33</b>	<b>AY534400</b>	<b>AY534478</b>
<i>Cribrarula cribraria cribraria</i>	Linnaeus, 1758	15, 24, 38, 52, 53, 55, 59, <b>23, 50, 98</b>	AY161566	AY161800
<b>52. <i>Cribrarula cribraria melwardi</i></b>	<b>Iredale, 1930</b>	<b>50</b>	<b>AY534401</b>	<b>AY534479</b>
<i>Cribrarula cribraria rottnestensis</i>	Raybaudi, 1987	40	AY161568	AY161802
<b>53. <i>Cribrarula cribraria abrolhensis</i></b>	<b>Lorenz, 2002</b>	<b>38</b>	<b>AY534402</b>	<b>AY534480</b>
<i>Nesiceypraea Australiatica langfordi</i>	Kuroda, 1938	93	AY161516	AY161749

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<i>Nesioeypraea Austrasiatica hirasei</i>	Roberts, 1913		AY161514	AY161747	
<i>Nesioeypraea Austrasiatica sakurai</i>	Habe, 1970	25	AY161515	AY161748	
<i>Palmulacypraea katsuae</i>	Kuroda, 1960	25	AY161584	AY161818	
<b>54. <i>Palmulacypraea musumea</i></b>	<b>Kuroda &amp; Habe, 1961</b>	<b>55</b>	<b>AY534403</b>	<b>AY534481</b>	
<b>55. <i>Erronea xanthodon</i></b>	<b>Sowerby I, 1832</b>	<b>51</b>	<b>AY534404</b>	<b>AY534482</b>	
<b>56. <i>Erronea pallida</i></b>	<b>Gray, 1824</b>	<b>16</b>	<b>AY534405</b>	<b>AY534483</b>	
<b>57. <i>Erronea vredenburgi</i></b>	<b>Schilder, 1927</b>	<b>104</b>	<b>AY534406</b>	<b>AY534484</b>	
<b>58. <i>Erronea rabaulensis</i></b>	<b>Schilder, 1964</b>	<b>95</b>	<b>AY534407</b>	<b>AY534485</b>	
<b>59. <i>Erronea fernandoi</i></b>	<b>Cate, 1969</b>	<b>109</b>	<b>AY534408</b>		
<i>Erronea (Adusta) onyx</i>	Linnaeus, 1758	3, 14, 20, 57, 11	AY161608	AY161842	
<i>Erronea (Adusta) adusta</i>	Lamarck, 1810	5, 9	AY161610	AY161844	
<i>Erronea (Adusta) subviridis subviridis</i>	Reeve, 1835	55, 51	AY161612	AY161846	
<i>Erronea (Adusta) onyx melanesiae</i>	Schilder, 1937	54	AY161609	AY161843	
<i>Erronea (Adusta) subviridis dorsalis</i>	Schilder & Schilder, 1938	33, 38	AY161611	AY161845	
<b>60. <i>Erronea pyriformis</i></b>	<b>Gray, 1824</b>	<b>107</b>	<b>AY534409</b>	<b>AY534486</b>	
<i>Erronea cylindrica cylindrica</i>	Born, 1778	16, 24, 30, 33, 59	AY161607	AY161841	
<b>61. <i>Erronea cylindrica lenella</i></b>	<b>Iredale, 1939</b>	<b>55</b>	<b>AY534410</b>	<b>AY534487</b>	
<b>62. <i>Erronea ovum ovum</i></b>	<b>Gmelin, 1791</b>	<b>16, 23</b>	<b>AY534411</b>	<b>AY534488</b>	
<i>Erronea ovum palauensis</i>	Schilder & Schilder, 1938	57	AY161601	AY161835	
<i>Erronea erronea</i>	Linnaeus, 1758	11, 14, 16, 30, 52, 55, 57, 58, 33, 53, 56	AY161606	AY161840	
<i>Erronea ovum chrysozona</i>	Schilder, 1927	53, 54	AY161600	AY161834	
<i>Erronea caurica caurica</i>	Linnaeus, 1758	23, 30, 33, 38, 52, 53, 55, 64	AY161602	AY161836	
<i>Erronea caurica cf. derosa</i>	Gmelin, 1791	14, 11	AY161603	AY161837	
<i>Erronea caurica dracaena</i>	Born, 1778	9, 10	AY161604	AY161838	
<i>Erronea caurica quinquefasciata</i>	Roding, 1798	1, 3, 5	AY161605	AY161839	
<b>63. <i>Erronea caurica elongata</i></b>	<b>Perry, 1811</b>	<b>5</b>	<b>AY534412</b>	<b>AY534489</b>	
<b>64. <i>Erronea caurica spp. 1</i></b>		<b>3</b>	<b>AY534413</b>	<b>AY534490</b>	
<b>65. <i>Erronea caurica spp. 2</i></b>	<b>Lorenz, 2002</b>	<b>3, 11</b>	<b>AY534414</b>	<b>AY534491</b>	
<i>Purpuradusta serullifera</i>	Schilder & Schilder, 1938	55, 67	AY534415	AY534492	
<i>Purpuradusta minoridens</i>	Melville, 1901	69, 71	AY161578	AY161812	
<b>67. <i>Purpuradusta oryzaeformis</i></b>	<b>Lorenz &amp; Sterba, 1999</b>	<b>14, 32, 31, 98</b>	<b>AY161577</b>	<b>AY161811</b>	
		<b>69, 70</b>	<b>AY534416</b>	<b>AY534493</b>	

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OTUs	Authors	Sampled localities*	16S	Accession #	COI
<i>Purpuradusta microdon microdon</i>	Gray, 1828	52, 59, 56	AY161576	AY161810	AY161810
<b>68. <i>Purpuradusta microdon chrysalis</i></b>	<b>Kiener, 1843</b>	<b>5</b>	<b>AY534417</b>	<b>AY534494</b>	<b>AY534494</b>
<i>Purpuradusta hammondae</i>	Iredale, 1939	23, 38, 98	AY161579	AY161813	AY161813
<i>Purpuradusta gracilis notata</i>	Gill, 1858	3, 5	AY161581	AY161815	AY161815
<i>Purpuradusta gracilis gracilis</i>	Gaskoin, 1849	14, 15, 20, 28, 33, 59, 11, 51	AY161580	AY161814	AY161814
<i>Purpuradusta fimbriata fimbriata</i>	Gmelin, 1791	5, 9, 14	AY161582	AY161816	AY161816
<i>Purpuradusta fimbriata unifasciata</i>	Mighels, 1845	30, 31, 59, 64, 69, 18, 19, 23, 61, 70	AY161583	AY161817	AY161817
<b>69. <i>Purpuradusta fimbriata marquesana</i></b>	<b>Lorenz, 2002</b>	<b>71</b>	<b>AY534418</b>	<b>AY534495</b>	<b>AY534495</b>
<b>70. <i>Purpuradusta fimbriata waikiensis</i></b>	<b>Schilder, 1933</b>	<b>73</b>	<b>AY534419</b>	<b>AY534496</b>	<b>AY534496</b>
<i>Contradusta walkeri</i>	Sowerby I, 1832	14, 23, 38, 98	AY161598	AY161832	AY161832
<i>Contradusta bregeriana</i>	Crosse, 1868	54, 92	AY161599	AY161833	AY161833
<b>71. <i>Contradusta? barclayi</i></b>	<b>Reeve, 1857</b>	<b>106</b>	<b>AY534420</b>	<b>AY534497</b>	<b>AY534497</b>
<b>72. <i>Contradusta? pulchella</i></b>	<b>Swainson, 1829</b>	<b>22</b>	<b>AY534421</b>	<b>AY534498</b>	<b>AY534498</b>
<b>73. <i>Notadusta? hungerfordi</i></b>	<b>Sowerby III, 1888</b>	<b>22</b>	<b>AY534422</b>		
<i>Notadusta martini</i>	Schepman, 1907	64	AY161590	AY161824	AY161824
<i>Notadusta punctata punctata</i>	Sowerby II, 1870	23, 52, 53, 55, 59, 64	AY161589	AY161823	AY161823
<b>74. <i>Notadusta punctata trizonata</i></b>	<b>Sowerby II, 1870</b>	<b>69, 70</b>	<b>AY534423</b>	<b>AY534499</b>	<b>AY534499</b>
<i>Notadusta punctata (Andaman)</i>	Linnaeus, 1771	69, 70	AY161588	AY161822	AY161822
<i>Notadusta punctata berinii A</i>		14	AY161587	AY161821	AY161821
<i>Notadusta punctata berinii B</i>	Dautzenberg, 1906	5	AY161586	AY161820	AY161820
<i>Melicerona listeri</i>		10	AY161585	AY161819	AY161819
<b>75. <i>Melicerona listeri melvilli</i></b>	<b>Gray, 1824</b>	<b>19, 30, 12</b>	<b>AY534424</b>	<b>AY534500</b>	<b>AY534500</b>
<b>76. <i>Melicerona felina</i></b>	<b>Hidalgo, 1906</b>	<b>50</b>	<b>AY534425</b>	<b>AY534501</b>	<b>AY534501</b>
<i>Eclogavena dayritiana</i>	Gmelin, 1791	3, 5	AY161596	AY161830	AY161830
<i>Eclogavena quadrimaculata thielei</i>	Cate, 1963	24	AY161591	AY161825	AY161825
<i>Eclogavena quadrimaculata thielei</i>	Schilder & Schilder, 1938	33	AY161592	AY161826	AY161826
<i>Eclogavena quadrimaculata quadrimaculata</i>	Gray, 1824	16, 24, 27, 32, 52, 57	AY161597	AY161831	AY161831
<i>Eclogavena coxeni</i>	Cox, 1873	54	AY161594	AY161828	AY161828
<i>Blasicrura pallidula pallidula</i>	Gaskoin, 1849	15, 17	AY161593	AY161827	AY161827
<i>Blasicrura pallidula rhinoceros</i>	Souverbie, 1865	32, 52, 54	AY161593	AY161827	AY161827
<b>77. <i>Blasicrura pallidula cf. vivia</i></b>	<b>Steadman &amp; Cotton, 1943</b>	<b>67</b>	<b>AY534426</b>	<b>AY534502</b>	<b>AY534502</b>
<i>Blasicrura interrupta</i>	Gray, 1824	14, 30, 12	AY161595	AY161829	AY161829
<b>78. <i>Blasicrura summersi</i></b>	<b>Schilder, 1958</b>	<b>92</b>	<b>AY534427</b>	<b>AY534503</b>	<b>AY534503</b>